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FIELD OBSERVATIONS ON RARE OR LITTLE KNOWN MAINLAND ANOLES

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ABSTRACT

Species of mainland anoles that have remained little known because of rarity, restriction to remarkably small geographic areas, inaccessibility of range or habitat, or similarity to a commoner species, include *Anolis anisolepis*, *A. cuprinus*, *A. dunni*, *A. gadovii*, *A. megapholidotus*, *A. microlepidotus*, *A. parvicirculata*, *A. subocularis* and *A. taylori* in Mexico; *A. aquaticus*, *A. attenuatus*, *A. biscutiger*, *A. carpenteri*, *A. dollfusianus*, *A. haguei*, *A. insignis*, and *A. rodriguezi* in Central America, and *A. aequatorialis*, *A. chloris*, *A. gemmosus*, *A. maculiventris*, *A. nigrolineatus*, *A. peraccae* and *A. princeps* in Ecuador. Field observations on each of these species are presented. Morphological traits (mean adult size and sexual dimorphism, weight, size and color of dewlap, relative lengths of tails and limbs) and behavioral and ecological traits (temperature preferenda, height and diameter of perch, season of egg-laying, display-activity patterns) are listed and discussed. In the past, several of the species have been considered subspecies of other species. In each instance status is discussed and evidence for full specific status is presented. Lack of close ecological counterparts between Mexico, Central America and Ecuador is demonstrated. The Ecuadorian series of species tends to arboreal habits, large size, and relatively long tails. The Mexican species tend to terrestrial habits, small size, and marked sexual dimorphism, with males usually larger than females.

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INTRODUCTION

Field studies of anoles have been carried on by us intermittently over an eight-year period in Mexico, Central America and northwestern South America with most concentrated efforts devoted to demographic investigations of several abundant species: *Anolis cupreus*, *A. limifrons*, *A. humilis*, *A. tropidolepis*, and *A. sericeus* (Echelle, Echelle and Fitch, 1971a; Fitch, 1972, 1973a,b,c, 1975; Henderson and Fitch, 1975). Also, considerable attention has been devoted to poorly known species of this genus of iguanid lizards, and these are the subjects of the present report. The objective has been to obtain information that will help to clarify the ecological and phylogenetic relationships of these species with the commoner and better known kinds, and will lead to a better understanding of anoline lizard biology.

Data were obtained on a series of field trips (Costa Rica, February-March, 1965, November 1967 to July 1968, August-September 1968, February-March 1969, August-September 1969, January-March 1970, February-March 1973, June-July 1973, February-March 1974; Guatemala, February-March 1971; Mexico, Guerrero, June-July 1971 and March 1972, Chiapas and Oaxaca, February-March 1972; Ecuador, February-March 1975). A. A. and A. F. Echelle participated in some of the field trips, but their main contribution to the present report has been photographing and analyzing the display-activity patterns of many of the species. Fitch is solely responsible for the display diagrams of *Anolis attenuatus*, *A. insignis*, and *A. maculiventris*, all of which are based on relatively few filmed sequences.

Some of the species were found only once, or on a few occasions. Others that are still little known, were found to be abundant at certain times and places. This report includes 25 species that have been mentioned few times in published litera-

ture. New information is presented about each, especially with regard to habits, habitats, and characters that can be seen or determined only in the living animal, such as color of eye, color and size of dewlap, body weight, and sexual dimorphism.

Relationships within the genus are exceedingly complex, and *Anolis*, with its plethora of species, has provided excellent material for study of evolutionary processes, illustrating adaptive radiation, parallel and convergent specializations, and character displacement. Also this group of lizards has provided exceptional material for ecological and ethological studies. The sympatric and syntopic co-occurrence of species in various combinations and various habitats has created excellent opportunities for investigating competitive relationships and partitioning of resources (Fitch, 1975).

This genus of iguanid lizards was originally described in 1803 by Daudin, who named several species. Additional species were named in the 1830's, and in every decade thereafter the list has continued to grow, until now approximately 150 species are recognized from the North, Central and South American mainlands, while at least 90 species and many subspecies are recognized from the West Indian Islands. Naming of the mainland species accelerated to its maximum rate in the 1860's and 1870's, then dwindled to a low point in the 1920's. However, more recently, the discovery and naming of new species has again increased, and has continued up to the present, with the prospect that many still remain to be discovered and described.

The insular West Indian species often occur in spectacularly high population densities, in situations where they are readily accessible for field studies. Mainland species generally occur in much lower densities, sometimes in remote and relatively inaccessible areas. Many of the species currently recognized are known from

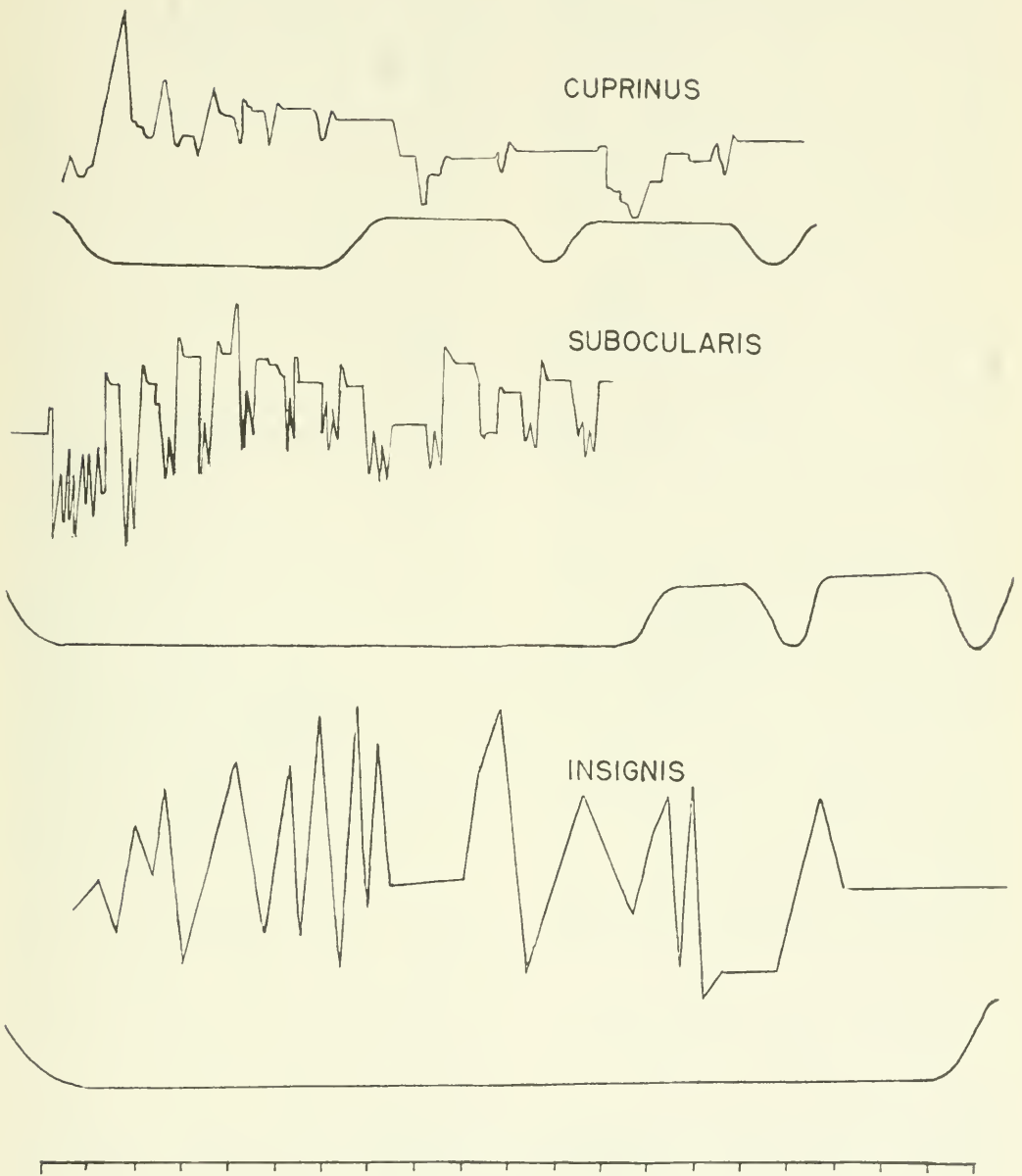


FIG. 1. Diagrams of Display-movements of Anoles. Upper line of each diagram shows vertical movements of head and lower line shows movements of dewlap. The metered line at bottom shows 1-second intervals. Upper: *Anolis cuprinus*, Zanatepec, Oaxaca Province, Mexico. Middle: *Anolis subocularis*, Marquelia, Guerrero Province, Mexico ("terminal" portion of display, which is sometimes given without initial portion). Lower: *Anolis insignis*, Monteverde, Puntarenas Province, Costa Rica.

only one locality or from few localities all within a small area. Many are known only from the original description, and some of these were described more than 100 years ago. Hence, in some instances, there is serious doubt whether a name represents a valid, but rare and elusive species, or was based upon an atypical or aberrant individual of a species already named.

ACKNOWLEDGMENTS

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METHODS AND MATERIALS

Tables 1-5 summarize ecological traits of the species studied insofar as these traits could be determined and also summarize characters of color and external morphology that are best observed on freshly collected or living anoles, but may be obscure or indiscernible on those that have been

long preserved. Table 1 is concerned with color, size and proportions: Color of dewlap and iris, mean tail-length as a percentage of snout-vent length, point reached by forwardly extended hind limb, mean snout-vent lengths and weights in adult males and females, and dewlap areas. Dewlap patterns are sometimes complex and when necessary are described in more detail in the species accounts. For the ratio of tail-length to snout-vent length, only individuals which seemed to have their original tails intact were included in calculating the means. The point reached by forwardly extended hind limb has provided a character much used in anoline systematics, but this character is much influenced by state of preservation and also is subject to individual variation. The limbs of hardened specimens are stiff and cannot be fully extended without breaking the bones and do not reach as far forward as in more flexible specimens. For this reason in the live anoles used for Table 1 the hind limb reached a little farther forward in some cases than indicated in published accounts based on preserved material. The adult snout-vent measurements and weights are intended to show typical sizes, which are poorly known even for most common species, and also to indicate trends of sexual dimorphism in size. In instances where few individuals were available, the size ratios of the sexes may be misleading and are subject to revision (*anisolepis*, *parvicirculata*, *chloris*) but in others represented by adequate series it is evident that males are larger (*cuprinus*, *gadovii*, *subocularis*, *taylori*, *dollfusianus*, *gemmosus*), that females are larger (*biscutiger*, *carpenteri*, *rodriguezi*), or that the sexes are very nearly the same size

FIG. 2. Diagrams of Display-movements of Anoles. Explanation as in Figure 1. Upper: *Anolis anisolepis*, San Cristóbal de Las Casas, Chiapas Province, Mexico. Second from top: *Anolis crassulus*, Panajachel, Guatemala, for comparison with the closely related *A. anisolepis* and *A. haguei*. Third from top: *Anolis haguei*, Quezaltenango, Guatemala. Bottom: *Anolis dollfusianus*, two populations; on left Tapachula, Chiapas Province, Mexico; on right Retalhuleu, Guatemala.

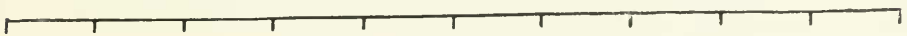
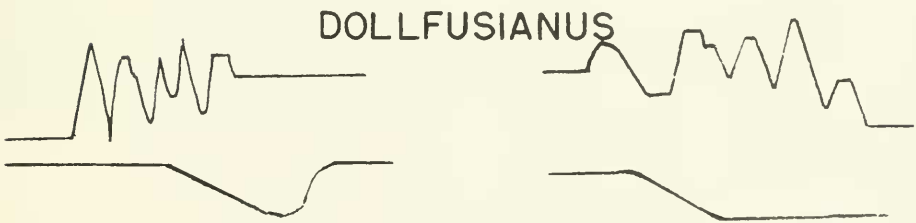
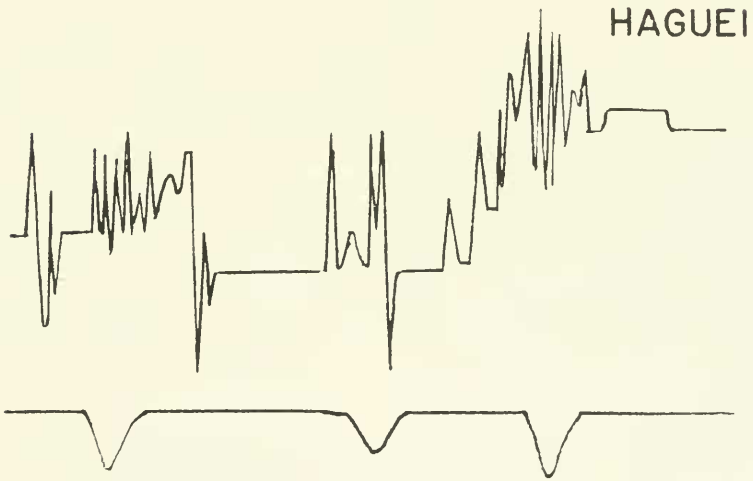
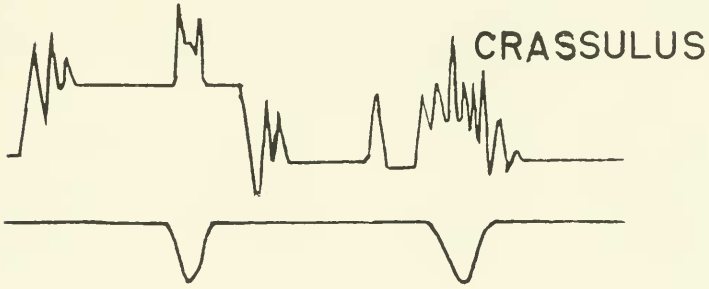
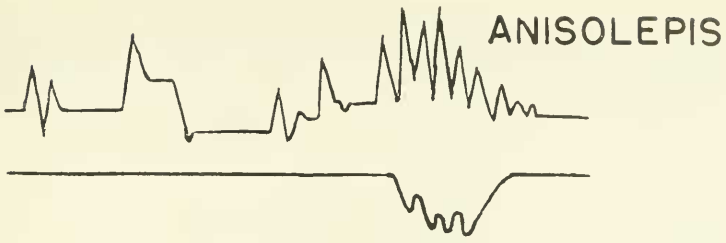


TABLE 1
MORPHOLOGICAL CHARACTERISTICS OF *Anolis* spp.

SPECIES	Color of dendap	Color of iris	Adult snout-vent length (mm)		% Tail- lengths to S-V	Point reached by forward extended hind limb	Dendap area (mm ²)		Weight (grams)	
			♂	♀			♂	♀	♂	♀
<i>anisolepis</i>	red; yellow edge	dark	53.0(2)	56.0(1)	186(2)	ear or beyond	3.5 (2)	3.9 (1)
<i>euprinus</i>	rose; tan edge	dark	63.3(22)	46.5(15)	176(14)	eye	606(22)	51(11)	4.6 (14)	2.4 (7)
<i>dunni</i>	red	dark	53.4(3)	44.7(6)	192(1)	eye	330(1)	3.2 (1)
<i>gudovii</i>	purplish pink; 8 dark purplish streaks	dark	70.6(10)	62.6(12)	173(10)	nearly to eye	650(5)	124(5)	5.0 (10)	4.2 (12)
<i>megapholidotus</i>	reddish orange; 2 rose bands	dark	44.2(7)	43.4(14)	173(13)	ear	141(6)	23(14)
<i>microlepidotus</i>	purplish red; pale edge	dark	41.0(1)	48.0(2)	175(2)	neck	1.9 (2)	2.2 (2)
<i>parvicirculata</i>	orange; central reddish spot	dark	46.0(1)	50.0(1)	178(1)	eye to nostril	40(1)	2.5 (1)
<i>subocularis</i>	red; pale edge	yellowish	51.0(49)	38.8(19)	175(42)	eye to nostril	312(31)	100(6)	2.8 (45)	1.9 (7)
<i>taylori</i>	purplish red; pale bands	dark	71.8(45)	57.0(21)	190(15)	eye	670(16)	53(12)	6.4 (24)	3.7 (20)
<i>aquaticus</i>	yellowish-orange; 4 red bands	blue	62.3(12)	59.7(10)	165(8)	eye	567(18)	7.8 (5)
<i>attenuatus</i>	dark olive brown	blue	84.5(24)	80.6(18)	219(31)	eye to nostril	788(2)	87(1)	10.7 (19)	10.9 (12)
<i>biscutiger</i>	cream; dark yellow center	dark	37.3(42)	39.4(33)	197(43)	eye to nostril	0.89 (15)	0.93 (8)
<i>carpenteri</i>	orange	dark	38.5(6)	40.4(14)	161	ear	150	0.70 (41)	1.00 (29)
<i>dollfusianus</i>	yellow; pale edge	dark	39.0(54)	36.7(42)	187(56)	eye or beyond	116(33)	1.28 (41)	1.14 (29)
<i>haguei</i>	reddish orange; yellow edge	dark	45.0(2)	185(1)	eye to ear	2.6 (2)
<i>insignis</i>	dull white; orange red streaks	dark	151.0(1)	192(5)	neck

<i>rodriguezi</i>	orange yellow	dark	43.3 (15)	43.7 (23)	190 (13)	nostril	133 (7)
<i>aequatorialis</i>	checkered light and dark brown	blue	82.2 (7)	80.0 (3)	258 (3)	beyond snout	797 (3)	...	10.5 (3)
<i>chloris</i>	dull yellowish white; pale blue anteriorly; dark scales	blue	53.3 (3)	58.0 (1)	188 (3)	ear to eye	402 (2)	...	1.72 (3)
<i>gemmosus</i>	yellow; streaked w/blue, white, green	blue	62.5 (38)	58.5 (28)	268	eye to nostril	433 (27)	...	4.1 (27)
<i>maculiventris</i>	rusty red	pale golden yellow	46.0 (1)	...	194 (1)	ear to eye	187 (1)	...	1.48 (1)
<i>nigrolineatus</i>	dull white w/black lines	yellow	50.9 (14)	48.0 (15)	201 (16)	neck	127 (14)	...	1.97 (15)
<i>peracae</i>	dull white; gray streaks	dark; blue inner rim	49.9 (21)	46.3 (9)	221 (12)	ear to eye	182 (16)	...	1.78 (15)
<i>princeps</i>	white anteriorly; greenish posteriorly	golden brown	117.0 (2)	...	211 (2)	beyond snout	1485 (2)	...	22.9 (2)
<i>sp.</i>	pale red; black spot	dark	70.0 (1)	73.0 (1)	214 (2)	eye to snout	400 (1)	94 (1)	6.2 (1)

(*megapholidotus*). The area of the dewlap was determined by tracing the outline on paper while the organ was held fully extended and then measuring it with a planimeter.

Table 2 summarizes information about body temperature (first three columns) and reproduction (last two columns). It shows mean body temperature, range of body temperature, and adjacent air temperature for several species. The fourth column indicates observed occurrence, by month, of individuals indicating reproductive activity: Females with enlarged follicles or oviducal eggs; and juveniles, or large young. Although most populations were not sampled throughout the year, breeding seasons are inferred (Table 2) from the observed occurrence of eggs and young, from the observed incubation periods and growth-rates of several species (Fitch 1973a), and from observations that, in general, dry weather inhibits reproduction of anoles and wet weather induces it.

Table 3 shows preferred resting places for each of the 25 species, whether at ground level (leaf litter, rock surface) or above ground (height, and kind of perch such as tree trunk, rocks, foliage or stem). Perch-diameter is shown for those that used stems. Table 4 is also concerned with perches, but limited to the nine species for which most data were available, with intraspecific comparisons of adult males, females and immatures.

Table 5 summarizes interspecific co-occurrences. The alphabetical series at the top of the page includes 16 of this study and eight other commoner species that co-occur and interact with them. Although interactions are still poorly known in most instances, relative size, abundance, and extent of distribution are indicated, because these are factors that might influence the outcomes of interactions. Ordinarily, larger species would tend to dominate or displace smaller ones. Interactions between a common and/or widespread

species and a rare and/or geographically limited species would be relatively important and perhaps critical for the latter, but relatively inconsequential for the former.

The displays were filmed with a Super-8 motion picture camera (Bolex 155 Macro-zoom) at a speed of 18 frames per second. A Bell and Howell Super-8 projector adapted for single-frame advancement was used in the analysis of the displays. Some of the displays filmed were induced in unconfined anoles by presenting them with a mirror or a tethered rival, others were filmed in Plexiglas enclosures when several individuals of the same species or different species were confined together. The aggressive displays of iguanid lizards are complex, stereotyped, and species-spe-

cific (Carpenter, 1961a, 1961b). These displays may reflect both genetic relationships and environmental factors (Echelle *et al.* 1971a). The displays have been filmed and analyzed in few kinds of mainland anoles, notably in *Anolis nebulosus* (Jenssen, 1971). It has been demonstrated by Jenssen that interpopulational differences in displays may exist, and T. A. Jenssen (pers. comm.) has indicated that certain species show a variety of displays that differ in basic form. However, in such instances, one display type is much more frequent than the others and may be considered *the* display. Various display modifiers may cause differences in detail, reflecting the motivational state of the lizard.

TABLE 2
DATA ON BODY TEMPERATURE AND REPRODUCTION OF *Anolis* spp.

SPECIES	Body temperatures when active	N	Air temperature when active	Observed occurrences of ovarian follicles (OF) oviducal eggs (OE) juveniles (J) and large young (LY)	Inferred breeding season
<i>anisolepis</i>				OE: Feb.	July-Sept.
<i>cuprinus</i>	30.7(34.3-26.2)	24	30.5	J: Sept.-Dec.	July-Sept.
<i>dunni</i>				OE: June-July	July-Sept.?
<i>gadorii</i>	30.5	1	30.9	OF, OE: July	July-Sept.
				J: Feb.	
<i>megapholidotus</i>			17.5	OF, OE: June-July	June-Sept.
<i>microlepidotus</i>			21-17	OF, OE: July	July-Sept.
<i>parvicirculata</i>				OF, OE: Feb.	year round?
<i>subocularis</i>	31.4(34.6-28.0)	13	30.0	OF, OE: July	June-Oct.
<i>taylori</i>	29.1(32.8-26.2)	28	27.9	OF, OE: July	July-Oct.
				LY: Feb., Mar.	
<i>aquaticus</i>				OF, OE: Mar.	year round?
<i>attenuatus</i>	21.5	1	18.0	OF: Mar., July, Aug., J: Sept., Oct.	year round?
<i>biscutiger</i>	31.0(32.5-28.5)	36	32.6-27.3	OE: Dec., Jan., Feb., Mar., May, Aug.	year round?
<i>carpenteri</i>	27.3	1	27.0	J: Nov.	year round?
				LY: Feb.	
<i>dollfusianus</i>	28.4(31.9-26.0)	31	27.6	OF, OE: Feb.	?
				J, LY: Feb.	
<i>insignis</i>			20.0	J: Mar.	?
<i>aequativalis</i>	22.3(24.5-20.1)	2	22.0	J: Feb.	?
<i>gemmosus</i>	21.0(29.3-18.2)	34	20.4		year round
<i>nigrolineatus</i>	29.9(30.5-29.4)	5	30.5	OF, OE: Mar.	Feb.-July?
<i>peraccae</i>				OF, OE, J, LY: Feb., Mar.	year round? low Oct.-Dec.
<i>princeps</i>	27.4	1	27.2		?
<i>sp.</i>	26.0(26.4-25.6)	2	26.0	OF, OE: Feb. J: Feb.	year round?

TABLE 3
RESTING PERCHES OF *Anolis* spp.

SPECIES	N	Ground level			Above ground				Stem	diameter (m)
		%	Leaf litter	Rock surface	%	Height (m)	Trunk of large tree	Rock	Foliage	Perch
<i>anolis</i>	5	80	++	20	.45	++	+	.171
<i>cuprinus</i>	30	17.8	++	82.2	1.01	++	+++	
<i>dunni</i>	2	++	+++	++	
<i>gadowi</i>	55	.25	
<i>megapholidotus</i>	11	45	+++	
<i>microlepidotus</i>	6	100	+++	++	
<i>purpuricincta</i>	1	100	+	+	
<i>subocularis</i>	63	6.4	+++	93.6	1.14	+	+++	.102
<i>taylori</i>	34	5.9	+++	94.1	1.46	++	+	
<i>aquaticus</i>	++	++	
<i>attenuatus</i>	52	7.7	++	++	92.3	2.00	+++	
<i>biscutiger</i>	6	33.3	+++	66.6	1.07	+++	
<i>carpentieri</i>	11	36.3	+	63.7	.90	+++	
<i>dolffusianus</i>	39	23.6	76.4	.70	+++	
<i>haguai</i>	100	+++	
<i>insignis</i>	1	100	2.50	+++	+++	
<i>rodriguezi</i>	7	84.7	.83	+++	+++	.357
<i>acuatorialis</i>	2	15.3	+	100	1.25	+++	++	.012
<i>chloris</i>	100	+	
<i>gemmosus</i>	67	100	1.74	+	++	
<i>maculicinctus</i>	1	100	1.20	+++	
<i>nigrolineatus</i>	24	100	.96143
<i>peracae</i>	18	5.5	94.5	1.90	+++ (cacao)	
<i>princeps</i>	2	100	.80	++	+++ (banana)	.050
<i>sp.</i>	2	100	2.01	+	+++	

TABLE 4
COMPARISON OF RESTING PERCHES OF NINE *Anolis* spp.

SPECIES	Male			Female			Immature			Total			N
	% ground		mean height (meters)	% ground		mean height (meters)	% ground		mean height (meters)	% ground		mean height (meters)	
	above ground	level		above ground	level		above ground	level		above ground	level		
<i>attenuatus</i>	96.4	3.6	2.2	84.2	15.8	1.8	100	0	0.5	7.7	92.3	2.0	52
<i>carpentieri</i>	100	0	1.4	66.6	33.3	0.9	50	50	.08	36.3	63.7	0.9	11
<i>cupreus</i>	94.7	5.3	1.1	66.6	33.3	0.9	17.8	82.2	1.0	27
<i>dollfusianus</i>	88.5	11.5	0.7	61.0	39.0	0.7	71.4	28.6	0.6	23.6	76.4	0.7	39
<i>gemmosus</i>	100	0	2.2	100	0	1.5	100	0	1.5	0	100	1.7	67
<i>nigrolineatus</i>	100	0	1.2	100	0	0.8	0	100	.96	24
<i>peraccae</i>	91	9	2.5	100	0	0.7	100	0	2.0	5.5	94.5	1.9	18
<i>subocularis</i>	100	0	1.1	60	40	0.8	6.4	93.6	1.1	63
<i>taylori</i>	100	0	1.6	75	25	4.7	100	0	1.4	5.9	94.1	1.5	34

ACCOUNTS OF SPECIES
THE MEXICAN SPECIES
Anolis anisolepis

This species was described by Smith, Burley and Fritts (1968) from 23 specimens collected at San Cristóbal de las Casas and several nearby localities in western Chiapas. In describing it the authors stated that its specific distinctness from the closely related and similar *Anolis haguei* was demonstrated by sympatry; both were found together between San Cristóbal de las Casas and Tenaja. The authors distinguished *A. anisolepis* from its near relatives *A. crassulus* and *A. haguei* by the following diagnostic characters.

A. anisolepis: Dorsal crest prominent (with scapular and sacral gaps); dorsal scales enlarged, with largest, at mid-back, about half the size of ventrals, gradually becoming smaller laterally and grading into granular scales of sides; dorsal stripe lacking; size relatively small (S-V up to 47 mm).

A. crassulus: Dorsal crest lacking; dorsal scales abruptly larger than small lateral scales, the largest about equal to ventrals, with lateral dorsals larger than median dorsals; dorsal stripe lacking; size relatively small.

A. haguei: Dorsal crest prominent (with scapular and sacral gaps); dorsal scales enlarged, with largest at mid-back about half the size of ventrals, gradually becoming smaller laterally and grading into granular scales of sides; dorsal stripe present; size relatively large (S-V up to 53 mm). As do all other Mexican species here discussed, *Anolis anisolepis* and its near relatives belong to the *Chrysolepis* species series of *Beta* anoles.

On 14 February 1971, we captured five *A. anisolepis* 4.5 km S of San Cristóbal de las Casas beside Highway 190. There had been frost on the preceding night (elevation approximately 2150 m), general ter-

Some rare or little known mainland anoles (left) and associated species (upper). For each co-occurrence the three symbols show whether associated species is: larger (+) or smaller (—) or less abundant (+) or more abundant (—), encompasses range (+) or merely overlaps it (—).

[illegible]

TABLE 5—(continued)

	<i>cupreus</i>	<i>haguei</i>	<i>humilis</i>	<i>intermedius</i>	<i>limbatus</i>	<i>polylepis</i>	<i>aquatorialis</i>	<i>chloris</i>	<i>gemmosus</i>	<i>maculiventris</i>	<i>peracca</i>	<i>princeps</i>	<i>sp.</i>
MEXICAN													
<i>anisocephalus</i>	—	+											
<i>cupreus</i>													
<i>dunni</i>													
<i>gadorii</i>													
<i>megapholidotus</i>													
<i>microlepidotus</i>													
<i>parvicirculata</i>													
<i>subocularis</i>													
<i>taylori</i>													
CENTRAL AMERICAN													
<i>aquaticus</i>						+							
<i>attenuatus</i>			+	+									
<i>biscutiger</i>			+	+		+							
<i>carpentieri</i>	+	+	+	+	+								
<i>dollfusianus</i>													
<i>haguei</i>													
<i>insignis</i>			+	+									
<i>rodriguezi</i>			+	+									
SOUTH AMERICAN													
<i>aquatorialis</i>									+	—			
<i>chloris</i>										—	+	+	+
<i>gemmosus</i>							+	—	?		+	+	+
<i>maculiventris</i>								+			+	+	—
<i>nigrolineatus</i>										—	+	+	—
<i>peracca</i>								+		—	+	+	—
<i>princeps</i>								+		—	+	+	—
<i>sp.</i>								—		—	+	+	—

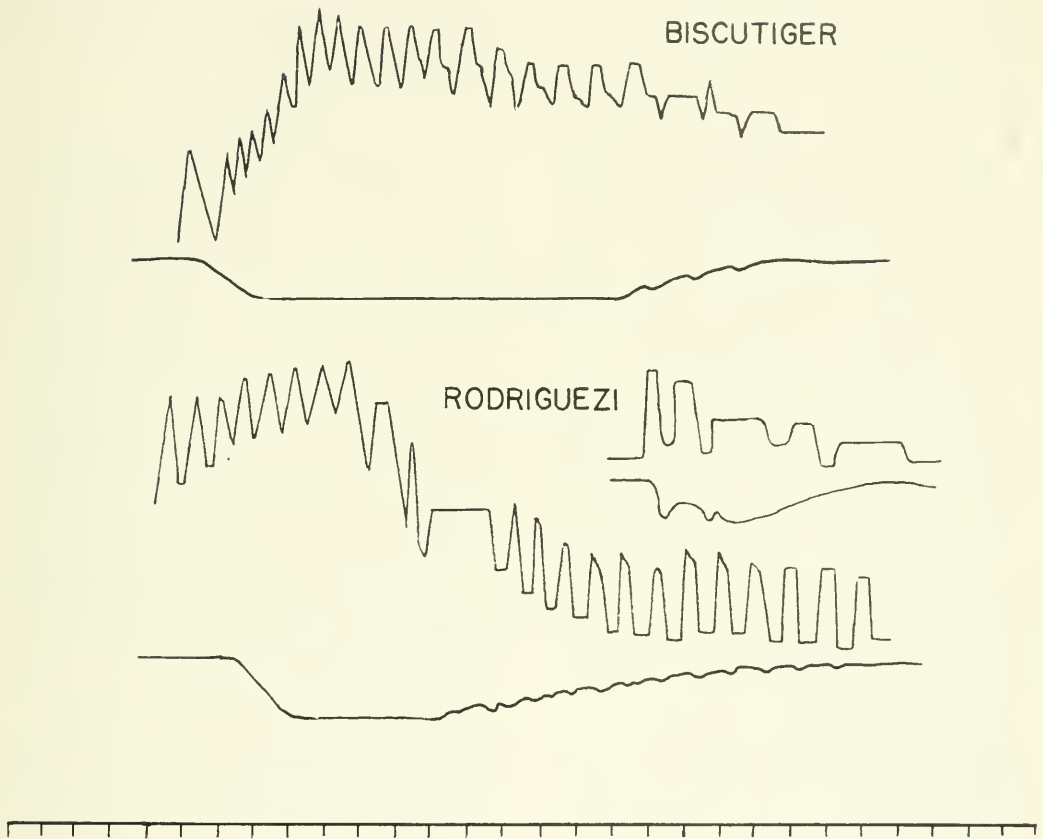


FIG. 3. Diagrams of Display-movements of Anoles. Explanation as in Figure 1. Upper: *Anolis biscutiger*, San Isidro del General, San José Province, Costa Rica. Lower: *Anolis rodriguezi*, Puerto Barrios, Izabal Province, Guatemala (typical display, and on right atypical short display).

rain was flat, open and xeric, but there was a roadside spring flowing into a marsh with vegetation including *Scirpus*, *Typha* and *Equisetum*. There was a dense thicket of *Crataegus*, with *Cornus*, *Sambucus*, *Smilax*, *Ribes*, *Salix* and other woody plants bordering the marsh along the road bank. The anoles were found, all within a 30 m radius, in this brush patch. One was on a horizontal stick .5 m over the spring, two were in dense grass at the edge of the marsh and two were in leaf litter beneath the bushes. They were relatively slow and clumsy and were easily caught.

The three adults each weighed between 3 and 4 grams and their lengths (S-V) were: 53 (♂), 53 (♂), and 56 (♀). All thus equalled or exceeded the maximum size indicated for *Anolis anisolepis* by Smith, Burley and Fritts (1968).

The only adult female among the five lacked oviducal eggs, but had somewhat enlarged ovarian follicles (diameter 5.6 left, 2.6 right). Absence of fully developed eggs and of young less than half-grown suggested a cessation of breeding for several months and from analogy with other species it may be inferred that reproduction of *A. anisolepis* is limited to the wettest part of the year (July-September).

The typical full display-activity pattern began with 1 (20.9%) to 4 (12.5%) preliminary sets of bobs—most commonly with 2 (41.6%) or 3 (25%) performed with the dewlap retracted. Duration of bobs of these preliminary sets was as follows: Set I, $.52 \pm .075$ sec ($n = 9$); Set II, $.26 \pm .063$ sec ($n = 8$); Set III, $.70 \pm .042$ sec ($n = 5$). A bobbing series followed (mean duration, $1.53 \pm .121$ sec, $n = 23$) during which the dewlap was pulsed in and out one to five times (usu-

ally three or four times). Duration of the entire display was $5.2 \pm .39$ sec ($n = 16$). Six of the 22 filmed sequences included no preliminary series of bobs and the figures for total time do not include these. The number of bobs per unit were noted for eight additional filmed sequences, although these were not analyzed frame by frame. In Figure 2 a display of *A. anisolepis* is compared with those of *A. crassulus* and *A. haguei*.

Anolis cuprinus

The original description (Smith, 1964) was based on a single adult male from near Zanatepec, Oaxaca, stated to be a member of the "*cupreus* group" closely related to *Anolis cupreus* of the west coast of Central America, but larger (53 mm S-V), with a distinct frontal concavity, having interparietal smaller than ear opening, having a "bright, blood-red dewlap," not bicolored as in *A. cupreus* and differing in a few details of lepidosis. Lynch and Smith (1966) reported a series of 26 from the same area as the type, and agreeing with it in most characters. Henderson and Fitch (1975) compared the structural niche of *Anolis cuprinus* with that of the smaller, syntopic *A. sericeus*.

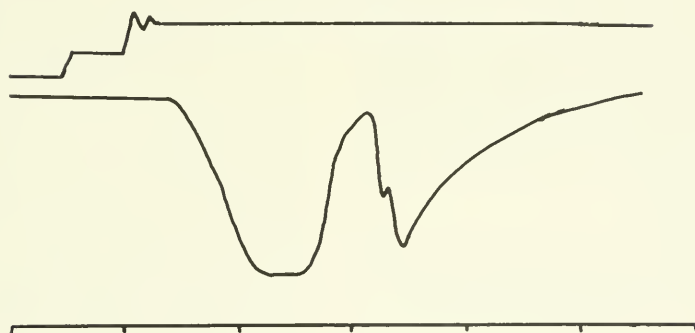
Collections were made on 10 and 22 February 1972, at Rancho Las Vigas, 8 km E Zanatepec, Oaxaca, Mexico. This locality is a relatively humid wooded canyon between 270 and 340 m elevation. Although the type locality was stated to be Zanatepec in the original description, intensive search by us near the town failed to reveal *Anolis cuprinus* there and the locality is in open, arid terrain of the coastal plain at an elevation of 240 m. In the original description Smith stated that

FIG. 4. Diagrams of Display-movements of Anoles. Explanation as in Figure 1. The diagrams for *Anolis taylori* and *A. dunni* shown here indicate relative amplitudes of dewlap and head movements (unlike other diagrams in Figs. 1-3 and *A. gadovii* in Fig. 4). Upper: *Anolis gadovii*, Tierra Colorada, Guerrero Province, Mexico. Middle: *Anolis taylori*, Puerto Marqués, Guerrero Province, Mexico. Lower: *Anolis dunni*, Palo Blanco, Guerrero Province, Mexico.

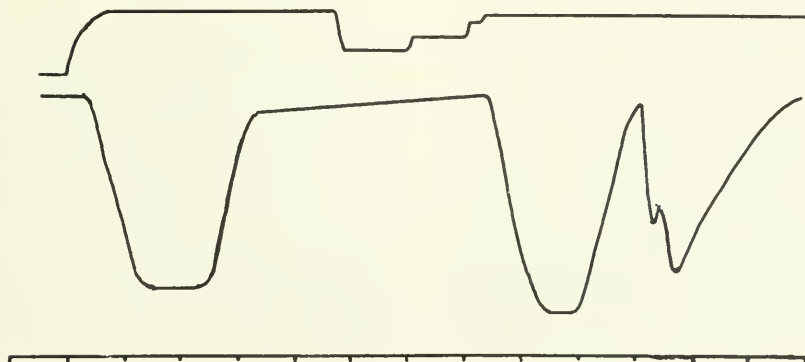
GADOVII



TAYLORI



DUNNI



the holotype was from 5,000 feet (about 1575 m) elevation, which suggests that the locality must have been several kilometers removed from Zanatepec, in the Sierra Madre to the north. Our specimens agree well with the description of the holotype in most respects, but in Smith's photograph the holotype has much more prominent transverse dark bands on the body and more dark pigment on the ventral surface.

The population found by us was limited to a few hectares at the head of a small canyon. Doubtless there are other localized populations in the same general region, but adjacent canyons were drier, with much evidence of fire, and none of the lizards could be found in them. Many *A. cuprinus* were found on the ground in leaf litter. Others were found on vertical tree trunks and stems, usually suspended head downward within 2 m of the ground. A few were on the vertical rock-faces of cliffs or outcrops.

All *A. cuprinus* were found within a few meters of the ravine bottom where there were large boulders and a trickle of water even at the height of the dry season. Even here there were signs of fire; trees, including large ones, had been partly burned. Some of the anoles found were on charred wood. Burning evidently had occurred within the previous year. Perhaps the lizards were able to escape incineration only in unusually protected situations such as were provided by the ravine bottom, but anoles that wandered onto the adjacent exposed slopes probably would have been killed off whenever burning occurred.

Most of the 37 *A. cuprinus* collected in February 1972, were adult, as were others seen that escaped, but a few were sub-adults. Evidently there had been no reproduction for many months—since the rainy season. The females had neither enlarged follicles nor oviducal eggs at this time, at the height of the dry season. Lynch and

Smith (1966) noted that their series of 26 collected between 6 September and 10 December consisted of adults and juveniles. Probably egg-laying begins soon after the onset of the rainy season (July?) and continues into September or even October, but ends in time for all but the latest eggs to develop into adults by February. If so, the annual cycle is like that of the more southerly *Anolis cupreus*, but with the breeding season even more concentrated by the constraints of the long and severe dry season.

Several males that were confined together displayed, and three sequences of different individuals were analyzed (Fig. 1). The displaying lizard tilted its head far back to allow ample space for extension of the relatively large dewlap, which was sometimes tipped or wobbled to make it more conspicuous to a nearby adversary. There was a series of 7-10 bobs (3.9-7.6 sec), a pause (.7-1.2 sec) and then three head drops with intervening pauses. Extension of the dewlap began with the first bob and lasted 5.3-9.6 sec, with retraction in the pause before the first head drop or immediately after it, lasting 2.7-3.2 sec. The dewlap was spread again between or after the head drops, for 1.0-1.9 sec, but not maximally. Following the second retraction by 2.1-3.4 sec was a third extension, .8-1.4 sec, after the last head drop. The bobbing sequence and head drops lasted 10.4-13.8 sec.

Anolis dunni

The original specimen, from Agua de Obispo "between Rincón and Cajones," Guerrero, was first reported by Smith (1933) as *Anolis gadovii*. Later the same author (Smith 1936) after having examined *gadovii* material, named the present species and distinguished it from *A. gadovii* by its widely separated, narrow and ill defined frontal ridges, vertically compressed nares, supraorbital semicircles broadly in contact, separated from inter-

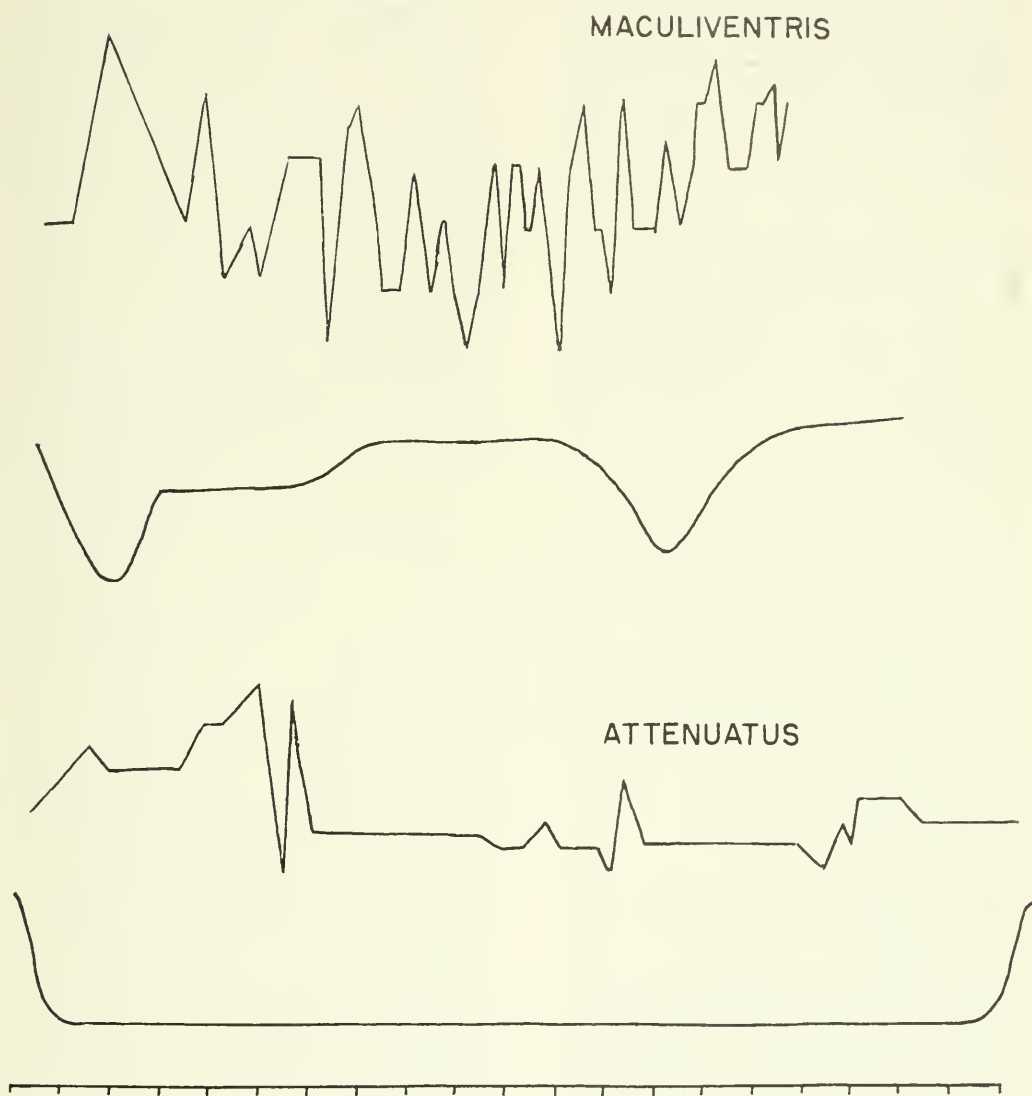


FIG. 5. Diagrams of Display-movements of Anoles. Explanation as in Figure 1. Upper: *Anolis maculiventris*, Tinalandia, Imbabura Province, Ecuador. Lower: *Anolis attenuatus*, Monteverde, Puntarenas Province, Costa Rica.

parietal by a single series of scales, and reddish dewlap. Davis (1954) mentioned additional characters. Davis and Dixon (1961) reported *A. dunni* from the same part of southern Guerrero, at elevations between 2,800 and 3,300 feet, in tropical deciduous forest and pine-oak forest adjacent to it at higher elevations. Duellman (1961) reported it 300 km farther west in Michoacán.

On 24 July 1971 an adult male was found in the lichen-covered crotch of a tree 2.13 m above ground in a humid canyon near a stream 7.5 km S Palo Blanco, Guerrero. A gravid female was found on the same day about .5 km down the same ravine on the ground in herbaceous vegetation at the edge of the water. No others could be found in a week of field work in the general area. Davis and Dixon (1961) found fully developed eggs in several females taken in June and July. Evidently the breeding season begins after the onset of summer rains.

In life the male was olive brown with a lateral white stripe on each side beginning behind and below the eye on the supralabials and ending above the thigh insertion. There were four pairs of lateral white spots on the body, each about the size of the ear opening, the first, on the shoulder, twice as high as long, and the others successively more rounded. The ventral surface was dusky, with small and obscure white dots. Dewlap coloration consisted of four or five dark red bands on a lighter red background; the bands ran parallel with the free edge of the dewlap.

The single male that we collected in July 1971 was kept alive for several months, and he displayed vigorously whenever other anoles were placed with him. The display (Fig. 4) was almost identical to that of *Anolis taylori*, having the same three dewlap movements, preceded by several shallow head jerks. In three of the four displays analyzed there was a preliminary extension of the dewlap preced-

ing the final three dewlap movements by 3.9 to 4.6 secs.

Anolis gadovii

This species was named by Boulenger (1905) from a specimen collected by H. Gadow at Tierra Colorada, 300 m in the mountains of southern Guerrero. It was not mentioned again in the literature until Mosauer (1936) rediscovered it and published a brief account of the habitat and saxicolous habits. Davis (1954) in describing *Anolis omiltemanus*, *A. subocularis* and *A. microlepidotus* from Guerrero, compared each with *A. gadovii* and included the latter in his key to Guerreran anoles. He characterized *A. gadovii* as large (up to 80 mm S-V), with long hind limb (reaching nearly to eye), having upper parts gray with dark markings, dewlap reddish, ventrals smooth, and with four gulars between the anterior chin shields.

Our observations on *A. gadovii* were made at Tierra Colorada, especially on a rocky hillside 1 km N Palo Gordo (an outlying village southeast of Tierra Colorada) in July 1971. The lizards were on steep rocky hillsides where there were loose boulders 1.5 to 4 m in diameter, sometimes in several layers with luxurious vegetation (including gnarled trees) growing among the rocks and vines screening some of the rock-faces. The anoles were extremely abundant. All were adults, usually associated in pairs, with intervals of usually 5 to 8 m between pairs. Most often the anoles were on vertical rock surfaces. They were shy and elusive, hiding beneath concealing vines and relying on their cryptic pattern, or moving downward out of sight and out of reach beneath the rocks. "An estimated 25 per cent of those seen used tree trunks or stems ranging from 2 to 50 cm in diameter" (Fitch and Henderson, 1976).

All the females seen appeared to be gravid. Ten that were dissected had

both oviducal eggs and enlarged follicles. Seven had an oviducal egg (10.5 to 14.6 mm) in each oviduct, and one enlarged follicle. The remaining three each had an oviducal egg on one side only and had a single follicle on the side opposite to the egg.

We revisited Tierra Colorada and Palo Gordo in the dry season, in February 1972. Trees were bare and leafless then and herbaceous vegetation was withered and dry. In prolonged search only three juveniles were seen. Evidently activity is much reduced, the anoles tending to stay in relatively cool and humid situations deep beneath the rocks. The breeding season of *A. gadovii* is believed to resemble that of *A. taylori* (July through October?) but to be even more restricted by the more xeric conditions where it occurs.

Five displays of two individuals were analyzed. The displays were characterized by one or two dewlap extensions each associated with a short series of ascending head bobs (Fig. 4).

Anolis megapholidotus

This species was described by Smith (1933) from four males and two females, all from Agua de Obispo about 45 km S Chilpancingo, Guerrero, Mexico. The species was diagnosed as having ventral and dorsal scales strongly keeled, scales of supraorbital semicircles enlarged, strongly keeled and in contact or separated by a single row of scales, occipital about equal in size to ear opening, dorsal scales larger than ventrals; dewlap red, extending to mid-belly in male, small in female.

Davis (1954) included *Anolis megapholidotus* in his key to Guerreran anoles and compared it with other species. Davis and Dixon (1961) found *A. megapholidotus* at additional localities near Agua de Obispo, in tropical deciduous forest and pine-oak forest, from 850 to 1350 m.

Females they collected in June were all gravid. Eight adult females we collected

at Agua de Obispo 10-12 July, 1971, also were all gravid. Four had one oviducal egg, each in the left and right oviducts and four others each had an egg in only one oviduct. Also, each female had either one (in 3) or two (in 5) enlarged ovarian follicles. Only adults were seen, suggesting that there had been no reproduction for several months during the dry season. Meanwhile, young of the previous year had grown to adult size.

Displays were easily elicited when males were confined together, but also were readily interrupted by movements of other lizards, and no fully complete sequences were filmed. Displaying males spread their small, brightly colored dewlaps to the fullest extent and, with head elevated, strained upward in several slow, irregular, bobbing movements. The dewlap movements were the most conspicuous part of the display. The dewlap was gradually and fully extended during the first 1.2 seconds, then collapsed, and finally gave three double pulses, each shorter and more rapid than the previous one, in the final three seconds. The entire display lasted approximately five seconds.

Anolis microlepidotus

This species was described by Davis (1954) from three specimens collected in the mountains of southern Guerrero near Chilpancingo, and was characterized as small and slender, with short legs, small ear opening, keeled ventrals, small keeled dorsals, grayish coloration, and ruby red dewlap. Davis and Dixon (1961) reported it from additional localities in the same general area. They found it in pine-oak and tropical deciduous forest types, in both xeric and swampy habitats.

We found *Anolis microlepidotus* at several localities in southern Guerrero and Oaxaca, at medium altitudes in rocky open woodland of scrub oak (*Quercus* sp.). The lizards were always associated with leaf litter and were at or near ground level.

An adult female found 4 km S Almolonga, Guerrero, June 1971, was perched on a small flat boulder in a clearing; another was on a horizontal stick 75 mm above the ground. In the mountains of northern Oaxaca, 3.2 km E Ixtepeji at about 1830 m, an adult male was found in a ravine bottom and ran into the cavity at the base of a large oak tree before capture. Two immatures were captured along the same ravine the following morning. One was in a small brush pile of oak cuttings and one flushed in a thicket ran up onto the stem of an oak bush. On 8 February in the mountains south of Oaxaca .8 km N Portillo San Andrés, 2,220 m, a juvenile female flushed from leaf litter climbed 75 mm on an oak stem 13 mm in diameter. The sky was overcast and the lizard was active at air temperature of about 17° C.

In life, these lizards were dull-brown dorsally, reddish brown head contrasting with body, and dewlap bright purplish red. Their habitats were among the most xeric in which we have found anoles of any kind.

One of the females collected near Almolonga in early July contained in each oviduct an egg nearly ready to be laid (11.0 x 5.6 mm left, and 11.2 x 6.5 mm right) and also contained large ovarian follicles (6.0 mm left, and 2.7 mm right). The other had an egg only in the right oviduct (10.1 x 6.2), but had large ovarian follicles on each side (7.2 left, 4.5 right). Both females show concentrated egg production after the onset of summer rains. The presence of juveniles in February seems to show that egg-laying may continue into November, and perhaps incubation and early growth are much slower at the altitudes where *A. microlepidotus* occurs than they are in species of the neighboring lowlands and foothills.

When an adult male and two immatures were confined together they displayed several times. One sequence, filmed

from the adult male, may be complete. As in other species of Guerreran anoles the display was relatively simple and was notable for the dewlap movements. The displaying lizard did not greatly elevate its head as do some other kinds, and there was conspicuous antero-posterior rocking movement accompanying the display bobs. The display consisted of three slow and high bobs with intervening deep bows and with a pause preceding the last bob. Each bob was accompanied by an extension of the dewlap, about halfway on the first one, fully on the second and about three-fourths on the third. This main part of the display lasted for 9 sec. In the following 7 sec after the bobs there were two small dewlap pulses, the second barely perceptible.

Anolis parvicirculata

This species has been reported only in the original description (Alvarez del Toro and Smith, 1956) from two specimens collected at Suspiro (between Ocozocautla and Quechula) in west-central Chiapas, Mexico. The authors characterized the species as a member of the "heteropholidotus group," thus associating it with *Anolis heteropholidotus*, a slender, long-tailed, high-montane species of El Salvador. *Anolis parvicirculata* has smooth ventrals, and has small scales in the supraorbital semicircles.

An adult female, captured near the type locality (3 km NW Suspiro) 15 February, 1972, was in life olive drab dorsally with a narrow pale tan, middorsal line; ventral surface pale grayish brown with coarse faint speckling laterally; legs were of the same color as body with no discernible markings, but the fingers and toes had faint dark bands; the dewlap was small and uncolored.

This is an unusually slender species, most readily recognizable by the extremely large eye with dark iris. The female's length of 50 mm (S-V) equalled the length

of the paratype and exceeded that of the male holotype (46 mm). As in most other rain-forest species the male probably is little, if at all, larger than the female and may average smaller.

The female contained a full-sized oviducal egg and a large ovarian follicle, although females of several other species collected in the same month in Chiapas and Oaxaca in more xeric habitats were all nonreproductive.

Anolis subocularis

In the original description, Davis (1954) listed 100 specimens from Tierra Colorada and nearby localities in southern Guerrero. He stated that some of the specimens had previously been reported as *Anolis nebuloides*, but they were different from that species in having dorsal scales noticeably smaller than ventrals. Other diagnostic characters mentioned were: Row of small intercalated scales between suboculars and supralabials; ventral scales keeled; long hind leg, reaching forward beyond eye; dewlap orange or reddish (p. 4, but also stated to be ruby red, p. 6); males considerably larger than females. Davis stated that *Anolis subocularis* was the commonest anole in Guerrero below 1500 m elevation.

An adult male we collected at Puerto Marqués had the following appearance in life: Dorsal color yellowish olive, with narrow, jagged-edged lateral brown line from above axilla to above thigh on each side and a second lower line, from behind axilla to thigh; several whitish spots with dark borders on each side; two longitudinal ventrolateral rows of black dots; ventral surface dull white; five pairs of dorsolateral light spots with dark edges; broad, faint, dark bars on limbs, more distinct on toes; top of head spotted with black, largest spots in supraocular region; tail faintly banded; dewlap red, extending posteriorly to level of elbows.

We found *Anolis subocularis* at many

localities in southeastern Guerrero and southwestern Oaxaca, sometimes in great abundance, in a variety of habitats, as indicated by the following field notes in July 1971, and February 1972.

25 February, 12 km ESE Río Grande, Oaxaca, in oceanside coconut grove. Many anoles were found mostly among dried palm fronds on ground.

26 February, .8 km N Guachupin, Oaxaca. East-facing hillside with open type of scrub forest (trees leafless then in dry season) interspersed with gigantic boulders, some in groups. Anoles were found on bare rock-faces and on tree trunks, within 1 m of ground.

26 February, 9.0 km E Jamiltepec, Oaxaca. One juvenile found in thicket beside swift, rocky stream.

27 February, 7.2 km W La Estancia, Oaxaca. Low, rolling grassland, recently burned off. Along a gully, which then, in the dry season, had a mere trickle of water, there was a band of green vegetation, with trees, brush and some herbaceous growth. Anoles were abundant in ground litter and on stems and tree trunks near the ground.

27 February, Ometepe, Guerrero. One found at dusk beside swift, rocky, mountain stream.

28 February and 21 and 22 July, 12 km W Marquelia, Guerrero. Anoles were found in moderate numbers on coconut palms in an open grove. Most often they were between 1 and 2 m on the trunk, clinging head downward and were conspicuous from a distance. They were somewhat wary and upon approach of a person would ascend the trunk far out of reach.

29 February, Puerto Marqués, Guerrero. Several were seen on the steep mountainside (strewn with gigantic boulders, interspersed with gnarled trees and thickets). Here they were associated with the much more numerous *Anolis taylori* and the relatively scarce *A. uebulosus*. *A. tay-*

lori was most often on rock surfaces, whereas *A. subocularis* was here seen only on tree trunks.

21 July, 7.2 km ESE San Marcos, Guerrero. Three adults were taken and others seen on the trunk of an isolated large thorny tree at the edge of a cultivated field.

21 July, 14.3 km N Cruz Grande, Guerrero. Eight were captured and others seen on tree trunks in a riparian grove.

All those collected or seen in late February and late July were adults. The February specimens were sexually inactive, with neither oviducal eggs nor enlarged follicles and with fat bodies minute. All seven July females were sexually active with a total of 9 oviducal eggs and 13 enlarged follicles. All but one had an enlarged follicle in each ovary; three each had 2 oviducal eggs, three each had 1, and one had none. Evidently, breeding had begun within the previous month, after the onset of the summer rains. Breeding must be limited to late summer and early autumn, probably ending in October or even earlier, because young had all attained adult size by late February.

Sexual difference in size is much greater in *Anolis subocularis* than in most other mainland anoles. Mean female-to-male length ratio was 76.1%. Mean female-to-male weight ratio was 49.1% in February, but had increased a 83.5% in July when all females were gravid.

Six displays of four individuals were analyzed. Initial and terminal portions of the display were often given separately. The initial portion, less stereotyped than the terminal portion, consisted of three or four bobs, a pause (2.5-5 sec) and another bobbing sequence, sometimes followed by a third. The terminal portion (Fig. 1) consisted of 11-17 bobs. Between the first two major bobs of the terminal series there were 3-6 short, rapid bobs. Each major bob consisted of a rapid upward movement from which the head was low-

ered about one-third of the downward distance and paused .2-.6 sec before it lowered the remaining distance. The dewlap was spread and retracted three times during the initial portion of the display and four times during the following pause, and was maximally extended during the long series of terminal bobs. It was retracted after the last bob but subsequently might be pulsed two or more times.

Anolis taylori

This species was described by Smith and Spieler (1945) from eight specimens collected in the vicinity of Acapulco, Guerrero. It was stated to be a "rock anole" closely related to *A. gadovii* and *A. dunni*, separable from the former by having only 2 (rather than 3 or 4) gulars in contact with mental, and separable from the latter by having smaller ventrals and having 7 or 8 (rather than 6) scales between nasals. Smith and Taylor (1950) included *A. taylori* in their checklist of reptiles of Mexico, but the species seemingly has not been investigated further in the last 25 years. Fitch and Henderson (1976) described the structural niche and field behavior of a population of *A. taylori* at Puerto Marqués 7 km SE Acapulco. These lizards are extremely abundant in their chosen habitat of enormous boulders on steep, wooded mountainsides.

In late July (early in the rainy season) only adults and adolescents could be found. All of the 13 adult females dissected were gravid. Five had an oviducal egg on each side and also an enlarged follicle in each ovary; 2 had an egg on each side, but had an enlarged follicle in only one ovary; 5 had an egg in one oviduct and a large follicle in each ovary; and one had only one egg and (on the opposite side) an enlarged follicle. Reproduction seemed near a peak at that time, with eggs being produced in rapid succession. In late February and early March (late in the dry season) the population sample con-

sisted largely of immatures, mostly more than half-grown, and adult females were nonreproductive.

The incidence of reproductive females and young of various sizes indicated suspension of reproduction in the dry season, perhaps from November through June, and resumption of breeding in July, with hatchlings beginning to appear around August and continuing to appear into October or November. A relatively short and concentrated breeding season, as compared with those in other anole species, is indicated.

Fitch and Henderson (1976) recorded a mean of approximately 29° (26.0 to 32.8) for 30 body temperatures of *A. taylori*. Generally air temperatures were near these levels when the lizards were most active. Activity tended to reach a peak about mid-morning and was much reduced at mid-day with some tendency to increase again in late afternoon.

The display of *A. taylori* was distinctive in having the dewlap fully extended or in motion for the entire sequence and constituting the dominant component, whereas head movement was minimal, generally consisting of 3-5 preliminary twitches. The dewlap was first slowly and fully extended, then gradually retracted ($1.90 \pm .092$ sec, $n = 18$). The extension and retraction covered approximately equal intervals, with a slight intervening pause ($.64 \pm .092$ sec, $n = 18$) while the dewlap was held maximally extended. There was another slight pause ($.98 \pm .056$, $n = 18$) between the retraction and the pulse that followed, during which the dewlap was spread to no more than half its full extent. A third extension, usually to no more than three-fourths of full extent, ended the series ($1.58 \pm .198$ sec, $n = 18$). The pulse between the two major extensions ranged from a completely separate movement to a momentary pause in the second major extension. The active, pulsing movements rendered the dewlap-display highly

conspicuous. The final retraction of the dewlap was often much more prolonged than the retraction occurring after the first dewlap display. In contrast to the first dewlap extension, the final extension immediately graded into retraction with no pause after maximal extension (Fig. 4).

Some variation in the display was noted. The dewlap was occasionally extended once, before (5 displays) or after (3 displays) the sequence described. Usually there was a pause of two or more seconds between these extra dewlap extensions and the main sequence.

THE CENTRAL AMERICAN SPECIES

Anolis aquaticus

This species was described by Taylor (1956), who had one specimen from Palmar and two from Golfito, both in Puntarenas Province, Costa Rica. Diagnostic characters listed in the original description include: Heavy, dark, transverse bars wider than interspaces on body, limbs, and tail; dewlap, large, orange; tail compressed with a middorsal row of enlarged serrate scales; ventrals keeled and much larger than dorsals; scales of middorsal pair of rows on body markedly enlarged; suboculars separated from supralabials by two or three rows of small scales; three or four scale rows between supraorbital semicircles.

In our study many *A. aquaticus* were observed and others were collected and preserved at Finca Las Cruces near San Vito, Puntarenas Province, Costa Rica. All of the lizards were found along swift, flowing, rocky, mountain streams. Usually, they perched on rocks; sometimes they were on logs or sticks. They were wary and when approached they dove into the water, swam for distances up to several meters, and emerged in well concealed places, such as cavities beneath log jams or overhanging rocks, or in accumulations of drift.

Of 9 adult females collected at Finca Las Cruces, 14 March, 1974, two had neither oviducal eggs nor enlarged follicles, but the remaining seven were all reproductive. Four each had an oviducal egg on one side and an enlarged follicle on the opposite side. One had an enlarged follicle on each side (4.5 and 3.4mm), but lacked oviducal eggs. One had an oviducal egg (left), but no follicles. One had an enlarged follicle (5.9 mm, left), but no oviducal eggs.

In other species of anoles, it is most typical for a female to have two oviducal eggs simultaneously—one larger than the other and destined for earlier laying—with ovarian follicles also developing, ready to replace each egg soon after it is laid. The smaller number of such reproductive units in the females of *A. aquaticus* suggests that it has a lower reproductive potential, although rate of development and extent of seasonal change are not known. In both February 1973 and March 1974, young of various sizes were seen (though in small numbers), suggesting year-round reproduction, as might be expected in the consistently warm and humid climate where *A. aquaticus* occurs.

Anolis attenuatus

Taylor (1956) named this anole (as a subspecies of *Anolis woodi*) from three

specimens collected at Isla Bonita, altitude 1680 m, on the southeastern slope of Volcán Poás, Heredia Province, Costa Rica. Diagnostic characters that he listed in the original description include: Large size (S-V 78-83 mm); tail 2.4 times body length; ventrals keeled and slightly larger than dorsals; approximately 140 scales about body; postanals enlarged; extended hind leg reaching forward beyond eye; extended foreleg reaching back to groin; body dull-red with black markings; dewlap large, dark olive, with magenta scales.

Anolis woodi was described by Dunn (1940) from El Volcán, Chiriquí, Panama, from a single female specimen, but Taylor (1956) reported it from Cañas Gordas, Puntarenas Province, Costa Rica, and other specimens have been reported from several localities in the southern half of Costa Rica. *A. woodi* and *A. attenuatus* are both large, slender, long-legged and long-tailed anoles with large dewlaps. However, they differ in body size, relative sizes of the sexes, color of body and of dewlap, and relative length of tail and limbs (Table 6). In view of these numerous and trenchant differences and the fact that their known ranges are well separated, so that there seems to be no opportunity for geographic integration, they are best considered distinct species.

We found *Anolis attenuatus* at Monte-

TABLE 6
COMPARISON OF *Anolis attenuatus* TO *A. woodi*

	<i>A. attenuatus</i>	<i>A. woodi</i>
Geographic range	Cordillera de Tilarán and C. Central	Cordillera de Talamanca
Size S-V		
mean for ♂ ♂	84.5 in 24	80.8 in 4
mean for ♀ ♀	80.6 in 18	69.9 in 10
♀ to ♂ size ratio	94.4%	86.6%
Dorsal color	Dull red with black markings	Olive with rusty spots
Dewlap color	Dark olive or black	Bluish white at base, bordered with amber yellow; pink orange on outer edge
Approximate number of scales around mid-body	140	125

verde, Puntarenas Province, Costa Rica, 70 km W and 11 km N of the type locality; from March 1973 to March 1974, 49 records were accumulated, many of them by Dr. Richard K. La Val. Most of the lizards were found on tree trunks; a few were on the ground.

These lizards were slow-moving and depended largely on cryptic behavior and coloration to avoid detection. Once seen, they were easily captured. On many occasions those that were captured and released, or merely observed in the field, were seen again after intervals of hours in almost the same location and position.

In their montane habitat, mean air temperature was about 18° C at the times of capture. The seasonal distribution of females that appeared gravid (March, July, August, September, and October) and of immatures suggested year-round reproduction.

Taylor (1956) described the behavior of two of the original specimens from Isla Bonita, before they were collected, as follows: "... on the top of a tree fern ... fighting. The male with dewlap extended would attempt to bite the female. Then the female would retreat to another frond and shortly would return to attack the male ... who at all times had the throat fan extended. ..." In our study, presentation of mirrors and of transferred individuals and placing individuals together in confinement did not elicit display, except when a juvenile was placed with a juvenile *A. insignis* and responded to its challenge. The displays were notable for the small amount of movement and the long pauses, with the large, dull-colored dewlap held fully extended (Fig. 5). The single display analyzed lasted 20 sec, with initial, middle and terminal phases separated by pauses of about 3.3 sec. The first phase consisted of a slow elevation of the head and spreading of the dewlap, then a slight dip and pause (1.4 sec) and a high bob interrupted by a half-second pause

near the top, a very rapid dip closely followed by another high bob and dip. The middle portion following the first main pause, began with a small dip followed by a small bob, short pause, second dip and medium bob. The terminal portion consisted of a small dip and then a rapid small bob followed by a medium bob with a pause (.7 sec) at the top, a small dip, pause, and final retraction of dewlap.

Anolis biscutiger

Taylor (1956) named *Anolis biscutiger* from 11 specimens collected in Puntarenas Province, Costa Rica (Golfito 1—the holotype, Palmar 8, 24 km WSW San Isidro del General 2). Among the diagnostic characters mentioned were: Small size (length S-V less than 40 mm); tail twice snout-vent length; extended hind limb reaching between eye and nostril; two pairs of much enlarged postanals; supra-orbital semicircles separated by one scale row; seven loreal series. Taylor did not specifically discuss the relationships of *A. biscutiger* and *A. limifrons*, but his descriptions of the two differ only in minor details and obviously they are closely related. Savage (1973) in his list of the amphibians and reptiles of Costa Rica did not include *A. biscutiger*, but considered it a synonym of *A. limifrons* (pers. comm.). Williams and Smith (1966) recorded it from Julieta and this locality remains the northwesternmost record.

Accumulated evidence has led to a reconsideration of the relationship of *A. biscutiger* to *A. limifrons*. The differences between them, though small, are numerous and fairly constant. The known range of *A. biscutiger* is in the Pacific lowlands of Costa Rica from Julieta to Golfito, effectively separated from *A. limifrons* in the Caribbean lowlands by the mountain-mass of the Cordillera de Talamanca. The type locality of *Anolis limifrons* is Cucuyas de Veraguas, Panama. Fresh material from there is needed for

comparison with other populations, including those of *A. biscutiger* and Costa Rican *A. limifrons*. However, it is known that Panamanian *A. limifrons* differ in size, proportions, dewlap-color and scalation from both these Costa Rican populations.

Some characters of *A. biscutiger* which reflect its relationships are the following: Female-to-male length ratio 105.6%, males $37.3 \pm .332$ mm, 43-33 in 42, females $39.4 \pm .416$ mm, 44-36 in 33; tail to snout-vent ratio 1.96%, 1.77 to 2.18 in 43; postanals much enlarged in males; adpressed hind limb reaches between eye and nostril; adpressed forelimb reaches beyond snout.

A total of 33 body temperatures were recorded for *A. biscutiger* at Quepos. All but two were in the range 30-33 and nearly half were in the interval between 31 and 32. In samples collected at Quepos in December, January, February, March, May and August, most females were gravid and juveniles were not prominent in any of these samples. Hence, it seems that in the humid climate where *A. biscutiger* occurs, its breeding is extended throughout the year, or much of it, but probably with changing levels of incidence.

The display begins with a series of 3-18 bobs (duration, $2.5 \pm .47$ sec, $n = 11$) as the dewlap is slowly extended. A series of 2-5 inverse head bobs (Echelle *et al.*, 1971a) follows (duration $1.57 \pm .183$ sec), during which the dewlap is gradually retracted. The pause between the two parts of the display is short ($.12 \pm .051$ sec). The dewlap is pulsed submaximally during each down movement of the inverse head bobs, which are of small amplitude. The display is relatively short, averaging $4.3 \pm .46$ sec.

Anolis carpenteri

This species was described by Echelle, *et al.* (1971b) from 10 specimens collected at the Río Reventazón, Turrialba, Cartago

Province, Costa Rica. Distinctive features indicated were: Small adult size (35 to 45 mm S-V); grayish green color; buffy eye ring; female-to-male ratio 104.9 per cent; relatively short tail (1.61 times body length); hind limb extending to ear or slightly beyond; forelimb extending to midway between eye and nostril; and orange dewlap. Myers (1971) described the species (as *Anolis procellaris*) from a single male (illustrated with a photograph from life) from Veraguas Province, Panama. A fairly extensive range in the Caribbean lowlands of Central America is indicated. There is one specimen in the K.U. Natural History Museum from 10.5 km N and 9 km E Matagalpa, Nicaragua. One was seen, but not captured, at Beverly, Limón Province, Costa Rica, and numerous individuals have been captured or seen at Finca La Selva, Heredia Province, Costa Rica.

At the latter locality, females examined and released in February, April, August, October and November all appeared to be carrying eggs and probably there is some reproduction throughout the year.

In the display, an initial crouch was followed by a series of two to four ascending push-up bobs and these were followed by a series of four to six slower and more uniform bobs, with a distinct pause after each. In three of seven displays, there was a preliminary series of two to four low, short bobs before the ascending push-ups, but in the remaining four displays this preliminary series was absent. The dewlap was fully extended during the entire display, which lasted about 15 seconds. In two displays, the tip of the conspicuous, red tongue protruded from the mouth. A more detailed description of the display was included in the original description of the species (Echelle *et al.*, 1971b).

Anolis dollfusianus

This small Guatemalan species was

named by Bocourt (1873) from San Agustín, Volcán Atitlán, altitude 1200 m. Stuart (1955) made a detailed comparison of *A. dollfusianus* with *A. cupreus*, implying that the two might be closely related and might even intergrade, as their ranges seem to be complementary. He stated that *A. dollfusianus* occurs commonly in the upper part of the tropical zone between altitudes of 600 and 1500 m and is abundant in coffee groves. He erroneously stated that the adult male of *A. dollfusianus* is only 25 mm in snout-vent length. Other diagnostic characters which he mentioned were the yellow dewlap, keeled ventrals, rugose plates of occipital region, and anterior head shields with upturned edges and central keel, making them appear tricarinate.

Field observations indicate that *A. dollfusianus* occurs in high population densities in favorable habitats. However, it has remained little-known because of the small geographic range, extending from the vicinity of Escuintla in Guatemala west to the vicinity of Tapachula, Chiapas, Mexico, a distance of approximately 270 km, in a band of perhaps half that width, at low and medium altitudes on the south slope of the Sierra Madre del Sur.

Our field observations on *A. dollfusianus* were made near Retalhuleu, Guatemala, 16-24 February 1971, and Tapachula, Chiapas, Mexico 17 February 1972. At the Guatemalan locality four of the six adult females each had a single oviducal egg and an enlarged follicle in the opposite ovary. A fifth which lacked the oviducal egg had an enlarged follicle (3.4 mm). The sixth female had a follicle that was only slightly enlarged. Approximately half of the 64 anoles in this sample were immature, but only five were less than half-grown.

In contrast, the series of 53 from southern Chiapas had only six immatures (from half-grown to adolescent size), and only one of 13 adult females had an oviducal

egg, while one other individual had an enlarged follicle. Seemingly, the timing of reproduction is influenced by locality and weather. At low altitude in southern Chiapas, there was little reproduction in late fall and winter 1971-72, but at higher altitude in southwestern Guatemala in a somewhat cooler and moister climate in late fall and winter 1970-71, reproduction was maintained at a considerably higher level.

Fifty-five displays were analyzed, 41 from 14 males from near Tapachula, Chiapas, Mexico, and 14 from 9 males from Retalhuleu, Guatemala. The two localities are 75 km apart and average differences were discernible in the displays. The most common display was a series of 3-10 rapid low-amplitude bobs that averaged 2.32 ± 1.77 sec for the Guatemalan lizards and $2.93 \pm .222$ sec for the Mexican lizards and were accompanied by a single dewlap movement of $1.66 \pm .094$ sec (Mexican) or $3.2 \pm .30$ sec (Guatemalan). In the Mexican lizards, dewlap extension began $1.07 \pm .061$ sec before the end of the last bob and $1.19 \pm .140$ sec after the beginning of the first bob. For the Guatemalan lizards, corresponding figures were $2.28 \pm .198$ sec and $.66 \pm .111$ sec. Although dewlap extension was definitely more prolonged in the Guatemalan lizards, the displays in the two populations were essentially similar (Fig. 2).

Anolis haguei

In the original description of *Anolis haguei*, Stuart (1942) distinguished it from the closely related *Anolis crassulus* by its much smaller dorsal scales. Later the same author (Stuart 1948, 1955) relegated *haguei* to subspecific status, indicating that it replaced *Anolis crassulus crassulus* in cloud forests of Alta Verapaz, Guatemala at altitudes above 1300 m. Smith and Kerster (1955) reported a single specimen, allegedly from "Región Soconusco" in the Pacific lowlands of southern Chiapas,

Mexico, and suggested that *haguei* was a species distinct from *crassulus*. Smith, Burley and Fritts (1968) described *Anolis anisolepis* from San Cristóbal de las Casas in the mountains of central Chiapas, as a near relative of both *A. crassulus* and *A. haguei*, and recognized an '*anisolepis* group' of species characterized by small size and having scattered small groups of enlarged scales irregularly distributed over the sides where most of the scales are minute granules. Members of the *anisolepis* group also have strongly keeled ventral scales, enlarged dorsals, and knobby, rugose dorsal head scales. The diagnostic characters that distinguish *A. haguei* from *A. crassulus* and *A. anisolepis* are listed under the account of the latter species.

On 16 February 1971, four of these anoles were captured and many others seen in a roadside hedge of agaves 2.4 km west of Quetzaltenango, Guatemala. The lizards were active and shy, responding to approach of a person by running back toward the stalk at the base of the leaf. The long, rigid leaves with recurved spines along their margins provided effective protection. The dorsal pattern of grayish brown with a series of paired dark blotches rendered these lizards remarkably like *Sceloporus* in appearance and the impression was heightened by their behavior and by the xeric aspect of the habitat. Two females had neither oviducal eggs nor enlarged follicles, but they may not have been fully mature.

The display usually consisted of 4 or sometimes 5 series of rapid bobs interrupted by short pauses. The final or main series of bobs had more than the preliminary series. The first consisted of 2 quick bobs with no extension of the dewlap. The second was longer (average $1.24 \pm .089$ sec, $n = 11$) with 3 to 6 bobs and a pronounced dip of the head toward the end of the series. A dewlap flash of $.42 \pm .045$ sec, $n = 11$ accompanied this series.

Compared with the display of *A. crassulus* from Panajachel, Guatemala (Fig. 2), the display of *A. haguei* was more variable, with an apparent repetition of the second preliminary bobbing series of *A. crassulus*. Homology with the second series of *A. crassulus* was predicated on the form of the bobs and the fact that they were accompanied by a dewlap movement. The third preliminary series was the shortest ($.24 \pm .052$ sec, $n = 11$) and usually consisted of a single quick bob occurring within a second before the final bobbing series. The latter involved 4-10 bobs and another dewlap flash ($.61 \pm .065$ sec, $n = 11$). Twice in displays of high intensity, two deep bobs (adding 2.6 and 4.1 seconds to the duration of the display) preceded the main display as described above. During these bobs, the dewlap was extended, the mouth gaped, and the engorged red tongue was conspicuous.

Anolis insignis

This species was described by Cope (1871) from a specimen purportedly from San José, Costa Rica (collected by a Dr. Van Patten). Diagnostic characters mentioned were: Giant size (total length up to 440 mm, snout-vent 145); ventrals smooth; tail base compressed; extended hind limb short of ear; ear opening half size of eye; body light brown, with four transverse double bands of greenish blue, a large ocellate spot, greenish blue with brown center anterior to axilla.

Taylor (1956) did not find the species in the course of his extensive collecting in Costa Rica, but he cited published records including La Palma between Guapiles and San José, Cariblanco, Ballena, and El Valle, Panama. Peters and Donoso-Barros (1970) stated the range to be "Panama to Costa Rica in mountainous areas."

The single specimen obtained by us, at Monteverde, Puntarenas Province, Costa Rica, constitutes an extension of the known range northwestward into the

Cordillera de Tilarán. It was a hatchling and was on a horizontal branch 2.5 m above ground. Local people reported finding a giant anole, almost certainly *A. insignis*, on the ground in a road, near the same location. When approached it displayed but did not attempt to escape. Probably the rarity of *A. insignis* in collections results partly from highly arboreal habits and preference for large trees in dense primary forest.

In displaying, the juvenile male held his head aligned with the body or only moderately elevated, not tipped far back as in most other species, and the dewlap was not extended to its maximum. The display consisted of a long series of bobs, with either two or three pauses of from 1 to more than 2 sec at low points between successive bobs. In each of two series, duration was 20 sec and there were 13 bobs (Fig. 1).

Anolis rodriguezi

This species was named by Bocourt (1873) from Panzos, Guatemala. Stuart (1948) discussed its similarity to *Anolis limifrons* of southern Central America and relegated *A. rodriguezi* to subspecific status under the former species. The range of *A. rodriguezi* extends from Central America into the Yucatán Peninsula, and various authors have commented on its distribution, habitat and lepidosis in that area.

Whether anoles of the *limifrons* species-complex occur uninterruptedly through the Caribbean lowlands from Costa Rica to Guatemala remains to be demonstrated, but there are extensive gaps in the known range and geographic intergradation between *rodriguezi* and *limifrons* has not been established. Seemingly, there are well-defined habitat differences. *A. limifrons* occurs in primary lowland rain forest and in edge situations. In Yucatán, Duellman (1963) found *A. rodriguezi* in great abun-

dance in xeric areas of scrub, but found it to be rare in rain forest.

Etheridge (1960), in his study of skeletal morphology of the anoles, found *A. rodriguezi* to agree with species of the *Chrysolepis* series, whereas *A. limifrons* and its near relatives were allocated in the *Fuscoauratus* series. In view of this discrepancy and other differences between the two (Table 7) it seems inadvisable to assign *rodriguezi* to the species *A. limifrons* without actual proof of intergradation. Differences in habitat, body size, proportions, sexual dimorphism, dewlap color and aggressive display provide further evidence against conspecificity of the two forms.

Two distinct types of displays were observed in *A. rodriguezi*. The more common display began with 2-5 preliminary bobs of $2.8 \pm .39$ sec, $n = 13$. The dewlap was then fully extended during an ascending series of bobs (2-17, most commonly 5, in 5.6 ± 1.7 sec, $n = 13$) followed by 2-3 descending bobs in $1.44 \pm .119$ sec, $n = 12$. Thereupon, the dewlap was partly retracted during a "plateau" bob ($1.78 \pm .169$ sec, $n = 11$), followed by 1-16 bobs with the head held alternately high and then low for approximately equal intervals, producing a rectangularly shaped bob. Mean duration of this series of bobs was 6.2 ± 1.21 sec, $n = 9$. During these bobs the dewlap was pulsed—outward as the head lowered and inward as it rose. The rectangularly shaped bobs closely resemble the "inverse head bobs" of *A. biscutiger* and those of *A. limifrons* described by Echelle *et al.* (1971a).

The less common type of display was observed only twice, performed by different individuals. These displays lasted 5.3 and 6.3 sec, and consisted of two rectangularly shaped bobs, a plateau bob, and two final bobs. The dewlap was extended for the entire display in one instance and was pulsed in the other (Fig. 3).

THE SOUTH AMERICAN SPECIES

Anolis aequatorialis

This large species was described by Werner (1894) with no more specific locality than "Ecuador." Peters and Donoso-Barros (1970), described the geographic range as "middle altitudes of western slopes in Ecuador," and they listed various diagnostic characters, including keeled ventrals, long hind leg extending beyond snout with tibia exceeding head length, smooth head scales and keeled supraoculars.

Williams (1974) mentioned that nothing was known of the habits of *A. aequatorialis*, but that, with *A. mirus* and his newly described *A. parilis*, it was a member of the *eulaemus* species subgroup of *Alpha* anoles. In this group, the toe pads are "Norops-like"—reduced as in strictly terrestrial kinds and not adhesive, so that the lizards are dependent on their claws for such climbing as they may do.

Five *Anolis aequatorialis* were captured at Tandapi, Pichincha Province, Ecuador on 18, 19 and 23 February, 1975. All were between 2 and 3 m above ground, on outer twigs or foliage of small trees or herbaceous plants. They were not wary or elusive, but seemed to depend on concealment for escape, and were well hidden by screening vegetation. They were found in the same sorts of situations as the smaller and much commoner *Anolis gemmosus*. Partitioning of resources was not evident.

A live, adult male was described as follows: Olive brown dorsally, with seven pairs of dark, dorsal chocolate marks each in the form of an elongate oval, meeting its counterpart middorsally in a chevron-like pattern; second series of oblique dark markings low on sides, partly merged with those of dorsolateral series; midventral area coppery; chin barred and speckled with black; supralabial region from loreals to ear dull white; limbs sharply barred; toes faintly barred; posterior half of tail black; top of head pale green spotted with black; large black patch with white specks on each side of neck; dewlap large, lacking bright colors but with strikingly checkered pattern of light and dark brown. A juvenile of 43 mm (S-V) was much like the adults in color and pattern, but the area between eye and ear, dull white in adults, was malachite green, and the chin was pale blue.

Anolis chloris

This was one of several species described by Boulenger (1898) from Paramba, Imbabura Province, in northwestern Ecuador. Peters and Donoso-Barros (1970) stated the range to be Pacific lowlands of Ecuador and Colombia, and Darién, Panama. They listed diagnostic characters, including keeled ventrals, extended hind limb reaching a point between ear and eye, supraorbital semicircles separated by two rows of scales, five rows of loreals, and six supralabials anterior to

TABLE 7
COMPARISON OF *Anolis rodriguezi* TO *A. limifrons*

	<i>A. rodriguezi</i>	<i>A. limifrons</i>
Geographic range	Yucatán Peninsula and northeastern Guatemala	Central America in Caribbean lowlands
Morphological relationships	<i>Chrysolepis</i> series of <i>Beta</i> anoles	<i>Fuscoauratus</i> series of <i>Beta</i> anoles
Size S-V		
♂ ♂	43.4 in 15	37.5
♀ ♀	43.7 in 23	38.6
♀ to ♂ size ratio	100.9%	102.9%
Dewlap color	Orange yellow	Dull white with faint yellowish central spot

center of eye. *A. chloris* is an *Alpha* anole of the *Latifrons* species series.

In late February and early March, 1975, three of these lizards were captured at Tinalandia, Río Pupusa, Pichincha Province, Ecuador, and several others were seen at the Río Palenque field station. All were adults. Dorsal color was emerald green. The dewlap was medium-sized, pale greenish with a pale blue outer edge. The eyes were blue and the tongue was orange. Those seen at the Río Palenque field station were all on balsa trunks, and only one was captured. Upon approach of a person the lizards would run several meters up the vertical trunks and escape. The sexes were not noticeably different in size.

Anolis gemmosus

This species described by O'Shaughnessy (1875, type locality unknown) was figured and further described by Boulenger (1885). It was included in the list of valid Neotropical anole species by Peters and Donoso-Barros (1970), who stated the range to be "lowlands of Pacific Ecuador" and summarized its scale characters and bodily proportions in their "matrix" for 116 anole species. Williams (1970) stated that its affinities were with other Ecuadorian species, the high-montane *Anolis andianus*, and *A. fasciatus* of the Pacific lowlands. All these are *Alpha* anoles of the *Latifrons* species series.

Despite Peters and Donoso-Barros' (*op. cit.*) statement, it is doubtful whether *A. gemmosus* occurs in the Pacific lowlands, as it seems to be a species of middle altitudes. It has remained poorly known. All published accounts are based upon preserved material, with erroneous statements concerning color and pattern.

In 1967, John D. Lynch and Robert W. Henderson, while carrying on field work on frogs at Tandapi, Pichincha Province, Ecuador, found *A. gemmosus* to be abundant there and they collected a large series.

Directed to Tandapi on Lynch's and Henderson's advice, we likewise found *A. gemmosus* to be fairly abundant on 18, 19, 23, 25 and 27 February and 15 March, 1975.

Much variation, individual, sexual and ontogenetic, was evident among the specimens collected, and those seen in the field. In life the general ground-color was deep emerald green. As in many other kinds of anoles, females often had a pale, longitudinal, middorsal band, but its occurrence and development was variable. The band was pale tan to rust color, usually set off by black margins, but these margins varied from broad to narrow. Among 21 adult females, nine had a broad dorsal band, two had a medium band, three had a narrow band, three had a broken or discontinuous band, two had remnants of a band and two were uniform-green. As in other species, the banded female pattern is already present in hatchlings. Though lacking the dorsal band, males were almost as variable as females in their dorsal patterns. Some were almost uniform-green while others were heavily spotted. Small, round or oval, buffy yellow spots were arranged in lateral, slightly oblique series, with as many as eight spots on each side in each series. Irregularly arranged black dots were also present on some, concentrated mainly in the ventrolateral area. Limbs were faintly barred, with black stippling on undersides of limbs and tail. Some white facial markings were present beneath the eye and extending onto the cheek.

In most populations of mainland anoles, male dewlaps are notably homogeneous in color and markings, but *A. gemmosus* is an exception. The highly-variable dewlaps did not seem to comprise well-defined classes but tended to form a continuum between extremes. At one extreme were dewlaps with little contrast, dull yellowish green on the basal area, shading to dull greenish yellow on the outer part. The

more contrasting and colorful type of dewlap was similar in having a dull greenish yellow outer part, but the basal part was bluish green with six narrow sharply defined white stripes diverging from a center on the anterior basal portion. The stripes had bright blue edges proximally at their origins, but distally the blue changed to green and the stripes themselves became suffused with the yellow background and finally blended into it and blended with their brighter colored edges.

In our sample of 70, only 13 were immature. Three were judged to be in their first two months (33, 28 and 27 mm) and three others, of 39, 38 and 37 mm were almost surely younger than six months old and more than two months old. The remaining six included four of adolescent size (53 and 52 mm, all females) and two that were more than half-grown (48 mm). A low incidence of reproduction through the fall and early winter months is indicated. However, at the time of sampling, in the rainy season, all females were reproductive. Seventeen each had two oviducal eggs; 11 each had an egg in only one oviduct and an enlarged follicle in the ovary of the opposite side; three each had only one oviducal egg, but no enlarged follicle; and three each had one enlarged follicle but no oviducal eggs. Some reproduction throughout the year is indicated, but with relatively low levels in the fall and early winter.

Anolis maculiventris

This small species was named by Boulenger (1898) from Paramba, northwestern Ecuador, and was stated to have a red dewlap, snout-vent length 45 mm, brownish and metallic purple dorsal color and smooth ventrals. Peters and Donoso-Barros (1970) listed additional characters: Frontal crests present; extended hind limb reaching between ear and eye; 3 or 4 series of scales separating supraorbital

semicircles; 8 rows of loreals; 8 supraoculars anterior to center of eye. *A. maculiventris* is a *Beta* anole of the *Fuscoauratus* species series.

A single adult male was found 22 February 1975 at Tinalandia, Río Pupusa, Pichincha Province, Ecuador, low on a tree trunk. In life it was dull grayish brown dorsally, with a pale rusty-red dewlap (having scales paler, yellowish), and with iris golden yellow. When confined with other male anoles, *A. chloris* and *A. peruccae*, this one displayed vigorously, although the others were unresponsive.

The display was complex, consisting of a long series of bobs (16 in 17 seconds) highly variable in amplitude and duration, with occasional short pauses in both the elevated and depressed positions. The first bob was the highest and shortest (2.5 sec) and the dewlap was slowly extended to a maximum corresponding to the peak of the bob. It was then retracted about halfway and held so for 2.5 sec, further retracted and held for 4 sec, and finally was slowly spread (not quite to the maximum) and retracted in the last 6 sec (Fig. 5).

Anolis nigrolineatus

This species was named by Williams (1965) on the basis of two specimens, from Machala and Guayaquil, El Oro Province, Ecuador. Williams (1974) mentioned two additional specimens from Playa de Montalvo, Los Ríos Province, Ecuador, and listed the following characters: Scales across snout 8 or 9; scales between supraorbital semicircles 1 or 2, loreal rows 4 to 7; scales between semicircles and interparietal 2 or 3; 7 to 11 supralabials anterior to center of eye; enlarged postnals in male; one middorsal scale row enlarged. Williams called attention to the swollen rostrum of *Anolis nigrolineatus*, projecting beyond the tip of the chin. He interpreted this development as indicating relationship to other anoles

having bizarre nasal appendages—*Anolis proboscis*, *A. phyllorhinus* and *A. laevis*. These, with *A. caquetae*, *A. dissimilis*, *A. nigrolineatus* and *A. punctatus* were considered to be near relatives comprising the *Punctatus* Group of *Alpha* anoles in the *Latifrons* species series.

On 10 and 11 March 1975, many individuals of this recently described species were observed in groves at the highway junction 5 km E Machala, El Oro Province, Ecuador. Males averaged larger than females (S-V $50.9 \pm .488$, range 55-47, and $48.0 \pm .390$, range 51-45). In life, the male was greenish with oblique rows of dark spots and fainter white spots on the sides and there was rusty suffusion on the sides and back of the head becoming fainter middorsally on the body. The undersurface was whitish with faint dark spots, with limbs and toes barred; the bars were formed from dark specks in a reticulate pattern; eyelids were buffy tan and iris was yellow. The chin was speckled with dull green. The tail was black for the middle third of its length. The dewlap was relatively small and of unusual shape, more than twice as long as deep when fully extended, dull white with a jet black horizontal line along its base on each side. The female was similar, except in lacking the dewlap, in having a pale tan middorsal stripe with a double dark line along each edge, and in having faint dark spots on the sides.

All the lizards seen were on cacao trees. They were shy and active, and at least half of those seen escaped. Most often they were first seen at heights between 1 and 3 m on the main trunks, but when approached they would dodge to the farther side of the stem and climb out of reach.

All that were seen were adults. Absence of young of any size indicated that there had been cessation of breeding activity for several months, for an interval that must have included fall and early winter.

However, 14 females dissected were all reproductive. Nine of them had an egg in each oviduct and the remaining five each had an egg in one oviduct and an enlarged follicle in the ovary of the opposite side. Thus, reproductive activity was near a peak at the height of the rainy season. However, southern Ecuador has a long and severe dry season and probably egg-laying does not occur during that interval.

Anolis peraccae

This species was described from Chimbo, Ecuador, by Boulenger (1898). Peters (1959) synonymized *Anolis irregularis* (Werner, 1901, type locality "Ecuador"), indicating that nearly all characters listed by the describer were identical, and that the details of pattern, arrangement of head scales and numbers of digital lamellae in which the two taxons differed were subject to much individual variation. Characters listed by Peters and Donoso-Barros (1970) for *A. peraccae* include: Smooth ventrals; frontal crests present; supraorbital semicircles contacting supraoculars, separated medially by one or two series of scales and separated from interparietal by 3 or 4 series of scales; 5 or 6 rows of loreals; 6 or 7 supralabials anterior to center of eye. *A. peraccae* is an *Alpha* anole of the *Latifrons* species series.

This small species was found to be relatively common and widely distributed in the lowlands of northwestern Ecuador. A total of 33 were captured in February and March 1975, at Santo Domingo de los Colorados, Río Palenque field station, and vicinity of Tinalandia, Río Pupusa. At least twice that number escaped. Compared with other small species, this one is extremely active and wary. Several were found on trunks of large trees in rain forest, a few others were on trunks of balsa trees and several were on roadside agaves. However, approximately 90 per cent were on banana trees. Most often the lizard was between one and three m above

ground on the banana stem, but at any movement in the vicinity it would run higher, having no difficulty in clinging to the smooth, vertical stems. Most ascended beyond reach and were lost in the crowns of the banana trees. Captures were made by using a straight pole, which was slowly extended until it touched the trunk above the anole. Then the pole was lowered along the trunk driving the lizard ahead until it had descended within reach, for capture by hand. Even those driven within reach usually escaped by running back up the stem, by jumping to another stem or leaf, or by finding shelter in a hole beneath the roots.

These anoles are dull and cryptically colored, with little difference between the sexes. The most conspicuous recognition marks were ventrolateral oblique dark streaks forming a fine grid-like pattern. The dewlap is relatively small in the male and absent in the female. Males were seen more often than females, probably because they perch in more exposed places. The 32 captured in late February and early March included 17 adult males, 10 adult females, 3 half-grown and 2 small juveniles. This high ratio of adults indicated a low level of breeding in the months before the sampling. Seven of the adult females were dissected and all but one were reproductive. Two each had oviducal eggs on both left and right sides; three each had one oviducal egg and an enlarged follicle on the opposite side; one had an oviducal egg but no follicle. This high level of reproduction, and scarcity of juveniles (only a little over 6 per cent of the sample) suggested recent increase from a low level of reproduction in fall and early winter.

Anolis princeps

Boulenger (1902) described this giant rain forest species from specimens from Río Lita, Paramba, San Javier, and Salidero, northwestern Ecuador. Peters and Donoso-Barros (1970) described the range

as lowlands of northwestern Ecuador, and mentioned the following characters: Dorsal color green with dark brown bars; ventrals not consistently keeled or smooth; extended hind limb reaching beyond snout; 4 or 5 series of scales separating supraorbital semicircles; 9 to 11 rows of loreals; 10 to 12 supralabials anterior to eye.

Two adult males were captured at the Río Palenque field station on 1 and 3 March 1975. In life they were olive green with two dark transverse bands on the neck and five more bands on the body, each consisting of a double series of five or six oval markings on each side (in both the anterior and posterior series). Some of the oval markings were like ocelli, having light centers. The ventrum was greenish white. The area around the eye was divided into alternate paler and darker sectors. The large dewlap was white along its anterior edge, ivory or slightly greenish white on its posterior part.

These large anoles were conspicuous on their low perches, and neither made any attempt to escape as the collector approached and captured them by hand. One was .8 m above ground on a stem .05 m in diameter, the other was 1.2 m high on a trunk of .8 m diameter.

Anolis sp.

In February, 1975, at Tinalandia, Río Pupusa, Pichincha Province, Ecuador, we found a species of anole that was obviously different from any described in published literature. Subsequently, at the Río Palenque field station, another specimen was found and the species was found to have been included in a key to the lizards of the Station, compiled by Kenneth A. Miyata of the Museum of Comparative Zoology, Harvard University. Mr. Miyata (pers. comm.) has informed us that the species is described in manuscript by E. E. Williams, and that it is tentatively asso-

ciated with *Anolis lemurinus*, a *Beta* anole of the *Chrysolepis* species series.

Distinctive features of the species are the short, blunt head (with rostrum especially shortened), long limbs and tail (Table 1), bold dark dorsal markings including a lyre-shaped occipital mark and a saddle-like sacral blotch and several intervening blotches on the olive ground color; dewlap that is relatively small and scarlet in the male, with a central black spot, about one-fourth as large and pink in the females, with the spot brown.

At Tinalandia an adult male was in a thicket at the base of a steep bank, climbing 1.6 m above ground on the terminal twigs of a shrub. A juvenile of 49 mm S-V was flushed from screening vegetation on the vertical surface of a high rock wall and ran several meters along the wall before capture.

An adult female (73 mm S-V) captured at the Río Palenque field station in early March 1975 was larger than the male (70 mm). This female contained two large oviducal eggs.

One seemingly complete display of the juvenile male from Tinalandia was filmed. It was relatively simple, beginning with a slow (4 sec) high bob which was followed by four that were lower and faster (2.0, 1.3, 1.9 and 2.0 sec). The dewlap was fully spread near the peak of the first bob and was partly retracted with each downward movement.

In view of the suggested relationship of this species to *Anolis lemurinus*, the display is of special interest for comparison with the latter. In five displays of three individuals of *A. lemurinus bourgaei* from Tikal, El Petén Province, Guatemala that were analyzed (A. F. Echelle ms) there were four slow bobs followed by a pause and then a final slow bob, with each elevation of the head accompanied by a dewlap extension—a pattern somewhat similar to that of the present species.

Displays of *A. lemurinus lemurinus*

from the vicinity of Escuintla, Guatemala, did not follow this basic pattern and were less similar to *A. l. bourgaei* and to the Ecuadorian species than these two were to each other. In each of four displays of the Escuintla anoles there were six bobs and one dewlap movement beginning at the end of the third bob or during the fourth bob, spreading maximally, then retracting at the end of the bobbing series (duration of display $3.4 \pm .52$ sec, dewlap exposure $1.51 \pm .047$ sec). Nine other displays were much more complex, with long ascending series and descending series of rapid bobs, with the dewlap maximally extended most of the time and spread one to three times per display. Display posture of *A. l. lemurinus* is distinctive. The head is pointed upward, and holding this position for long periods, the lizard occasionally flashes the dewlap in erratic fashion. The important differences between *A. l. lemurinus* and *A. l. bourgaei* in display and posture, dewlap, and body size cast some doubt on their supposed conspecificity.

DISCUSSION

The 25 kinds of anoles discussed above are almost equally divided among Mexican, Central American and Ecuadorian species, and the three geographic groups show some significantly different trends. Inasmuch as these three geographic areas are somewhat parallel in their range of climates, plant formations and agricultural crops, and each has many species of anoles, ecological equivalence might be expected among them. Each of the species included in this study and each of the better known common species in the same regions was compared with other species to determine the degree of ecological equivalence between the three regions.

For the common and dominant species of each region, especially, counterparts were sought that were similar in size, appearance, habitat and habits. One example

of ecological equivalence is that of the semi-aquatic *Anolis barkeri*, widely distributed in Mexico, and its counterparts *A. lionotus*, *A. aquaticus* and *A. poecilopus*, that are similar in size, habitat, and habits, in different parts of Central America. However, no other such clear-cut cases of ecological equivalence could be discerned.

In Central America the three most abundant species are *Anolis limifrons*, *A. humilis* and *A. cupreus*. The former is a species of the humid, Caribbean lowlands in forest and forest-edge. It is found on the ground in leaf-litter and grass, but also is scansorial on shrubs, tree trunks and vines. *A. humilis* of the same area, but extending from the lowlands up into cloud forest, occurs on the forest-floor generally in deep shade, usually in leaf-litter but often climbs on buttressed roots and tree bases. *A. cupreus* of the relatively dry Pacific versant is somewhat more scansorial than *A. humilis* and somewhat less so than *A. limifrons*. It is most typically found in leaf-litter of evergreen gallery forests near streams. All three species thrive in some types of disturbed and altered habitats as well as in primary rain forest and in fact all have been found in near-maximum abundance in cacao groves. Also, they have all been found in banana and coffee groves. *A. limifrons* and *A. cupreus*, but not *A. humilis*, have been found in coconut groves on the tree trunks. None of the three seems to have close counterparts among any of the Ecuadorian species. In Central America, *A. biscutiger* and *A. rodriguezi* are near relatives of *A. limifrons* that seem to replace it ecologically in some areas. *A. dollfusianus* is somewhat like *A. cupreus* and even more like *A. limifrons* in habits and behavior. In southern Mexico, both *A. subocularis* and *A. cuprinus* are much like the Central American *A. cupreus*, but both occur in more open and xeric situations. *Anolis sericeus*, widely distributed in Mexico and Central America, resembles *A. cupreus*

somewhat, but it is smaller and more slender and where the two overlap, at least, *A. sericeus* is definitely more scansorial. None of the three commonest Central American species (*A. limifrons*, *A. humilis*, *A. cupreus*) has an approximate equivalent in Mexico.

These three species, together with *A. sericeus*, *A. lemurinus* and *A. tropidonotus* occurring in both Central America and Mexico, and *A. nebulosus* and *A. subocularis* of southwestern Mexico, are all widely distributed and abundant, and sympatric with many additional species. Throughout Mexico and Central America one or another of the seven species mentioned tend to dominate habitats that are suitable for anoles and to exert selective pressure on other kinds that are less widely distributed and usually are less numerous in areas of co-occurrence.

The Ecuadorian species studied occurred in low population densities (only *A. gemmosus* was moderately abundant), were mostly medium to large *Alpha* anoles with little sexual difference in size, with arboreal habits, long tails, and with dewlaps often having white (4), green (3), and less frequently blue (2), red (2), and yellow (1). Most of them were notably shy and elusive.

In contrast the Central American species often occurred in high densities, were mostly *Beta* anoles of both *Chrysolepis* (5) and *Fuscoauratus* (2) series but with one *Alpha*. They ranged from extremely small to very large, were found at ground level or were scansorial low on shrubs and tree-trunks, had relatively short or medium-length tails, dewlaps usually yellow or orange, and had but little sexual dimorphism, with the female larger in several.

In the Mexican species, the trend was again somewhat different. Several kinds were found in high population densities, others were uncommon even in the limited areas where they occurred. All nine spe-

cies were *Beta* anoles of the *Chrysolepis* series, having short to medium tails, ground-living or rock-living habits (or if scansorial, occurring only on bushes and low on tree-trunks), small or medium size, dewlap often all red or partly red, sexual size-difference extreme in some, with males usually larger than females.

Divergent ecological trends in the three geographic groups may have some phylogenetic basis, with *Alpha* anoles tending to be larger and more arboreal and having longer tails. Also, climatic trends are closely correlated with the ecological trends observed. Most of the Mexican species have small geographic ranges or are even confined to a single locality within a few square kilometers. In those instances it seems that the populations are

relicts, surviving precariously in a region that is almost too xeric to support anoles. They have managed to survive only where local conditions mollify the aridity of the climate, and have undergone some adaptive specialization in the process.

In arid climates, such as are inhabited by most of the Mexican species, successful reproduction can occur only in the rainy season. Limitation of breeding to one part of the year intensifies its stresses. Males, needing to establish territories, repel rivals and find and court females, are selected for size, aggressiveness, and effectiveness of display. Sexual dimorphism becomes more pronounced than in the species that live in the relatively uniform and benign environment of a rain forest or cloud forest.

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